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THE JOURNAL OF ANIMAL BEHAVIOR

VOLUME 7, 1917

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JOURNAL OF ANIMAL BEHAVIOR

VOL. 7 JANUARY-FEBRUARY No. 1

NEW EXPERIMENTS ON THE LIGHT REACTIONS OF PLANTS AND ANIMALS[1]

CARL VON HESS

I

GENTLEMEN: Allow me, before the order of the day, to give a brief report of a discovery, which, though it stands only in loose relation to our theme, seems to me of general interest. I speak of the accommodation of the alciopids.

The alciopid is, as you know, a nearly transparent pelagic annelid, whose comparatively highly developed eyes have been repeatedly the object of histological research. It was believed that muscular elements could be demonstrated anatomically in these eyes and on this supposition theories of the act of accommodation were grounded. These theories can easily be proved mistaken, as the following shows; I will not further dwell on them.

On account of the small size of the eyes the largest—which I was enabled to examine had a diameter of hardly 1 mm.,—it had been considered heretofore impossible to attack the problem of their accommodative changes experimentally.

However, I was able, by laying the living and carefully isolated eyes on suitable electrodes, under seawater, and by observing them through binocular lenses in a very strong light falling from above, to follow the changes caused by electric irritation, and thus to discover a most remarkable accommodative process, unique in the animal world.

At another time I shall describe this process in detail, tonight I shall limit my description to the main facts.

---

[1] A lecture before the Morphological Society of Munich, reported and translated by Miss Hilda Lodeman.

If one views a fresh alciopid eye from in front, the surface surrounding the lens is seen to be threaded over with numerous fine silvery shining stripes, which have hitherto been mistakenly interpreted as muscles (Hesse). In fact these are structures which, like an iris, obstruct the passage of diffuse light into the eye; besides this, they make the eyes which are turned forward and downward, as invisible as possible to an enemy coming from below. They thus have the same effect as that which I some time ago proved to be the case with the silver sheen of fish.

Just below the lens there is a spot in the very soft eye-wall which, one may observe, contracts when the eye is stimulated; all the other portions of the tegument remain motionless. The lens, *when stimulated, moves forward perceptibly*, it approaches the cornea, as one may perceive most readily by looking at the eye in profile. Herewith is proved that the alciopids have an *active near accommodation;* for, by the above-mentioned contraction the distance between the lens and the retina is increased, while the lens remains unchanged in form. The way in which the change in the location of the lens is brought about is most interesting: The alciopids are distinguished from all other animals with otherwise similarly constructed eyes, by possessing a double vitreous body. Directly back of the lens we find a viscous fluid which is distinctly separated from the posterior space of the vitreous body and adheres closely to the walls of the eye on all sides. At the lowest point of this front part of the vitreous body the latter displays a curious ampulliform knob which is connected with the eye-water space by a canal and was formerly interpreted as an auditory sac by zoologists, and at present is supposed to be a gland belonging to the vitreous body for the secretion of its substance. My experiments show the real use of this protuberance. It occupies exactly the spot in the eye-wall in which alone contractile elements are found; the muscles, contracted, press the lump together like a rubber bulb filled with liquid, thus forcing a part of its contents into the eye, and slightly pushing forward the lens which rests in a bowl-like groove in the front surface of the vitreous body.

This is the second accommodative process among the invertebrates with which we have become acquainted; the mechanism differs entirely from that which I have proved Cephalopods to possess. Our observations teach anew how greatly physiological experiment can aid us in the interpretation of histological discoveries.

II

Among the lightreactions of Echinodermata which I have newly discovered and upon which I shall make only a brief report tonight, a certain interest attaches to those of the starfish, if for no other reason but that until now almost nothing of their sensitiveness to light was known. On the ground of anatomical research it was taken for granted that the familiar red points at the ends of their five arms were light receiving apparatus. Attempts to elucidate the question experimentally led to contradictory results. Some authors assert that those starfish which have an inclination to move toward the light cease showing this impulse after the tips of the arms with the " eyes " are cut off; according to other writers individuals thus mutilated still crawl to the light.

In the course of systematic experiments I discovered the surprising fact that the *feet of the Astropectinids are highly sensitive to light.* If light is flashed on them their little feet, relaxed in the dark, are instantaneously jerked in and the widely opened ambulacral groove is closed along the whole of the lighted area, the flanking white spines shutting over the incurled little feet. This startling phenomenon, which I was able to record in a number of snapshots, gave me the opportunity of examining the differing effects of colored lights. As with all the hitherto thoroughly examined invertebrates, it was found that colored lights have similar or identical relative values for our starfish as for the totally color-blind human eye; red lights remain almost or quite without effect even when very strong, while green and blue lights have a much stronger effect than the red lights, even when the latter seem to our normal eyesight much darker than the former. I was able also to prove adaptive changes in these starfish and to carry out exact measurements during my observations.

New and most remarkable light reactions in sea urchins were also disclosed. So far it had been known from experiments of Sarasin and Uexkull that some sea urchins raise their spine slightly when shaded from the light. More exact observations of their qualities of sight had not yet been made. I discovered the following interesting phenomenon appertaining to *Centrostephanus longispinus.* The animals have surrounding their aboral pole, 20 or 30 beautiful lilac colored, clublike processes about 3 mm. long, concerning which we knew hitherto only that they sometimes move in rotation, at other times are quiescent. I noticed that if a specimen at rest was slightly shaded, for example, if one's hand were passed quickly between window and reservoir, the little clubs began to rotate in a most lively manner. Further experiment showed that in order to bring about such agitation an exceedingly slight lessening of the lighting suffices. If, for instance, the greater part of the light reaches the animal from a gray pasteboard held at the proper angle, and I replace this board with one which is only a little darker in shade, the clubs begin to rotate quickly. Even with this method it was possible to a certain degree to make determining measurements, and I was able by the further use of differently colored boards for the lighting again to show convincingly that these animals also behave like totally color-blind human beings brought under corresponding conditions. Still more delicate, surprisingly exact measurements were made by using the method which I shall now describe.

III

Several writers have thought to deduce an argument against the experiments I have so far made with the qualities of sight in animals from the idea that I bring the " objective light-reaction " of animals into relation with the " subjective light sensation " of man. For anyone to whom the science of color is familiar, this argument is easily controverted. Still it is evident that there is a great advantage in showing that the problem may be attacked from quite a new direction. Therefore in a new series of experiments on a large scale, I brought the light sensitiveness of animals into relation, not to the " subjective light sensation " of human beings, but to the " objective light reaction " in the human eye, to the *changes in the size of the pupil* caused by light. This correlation was successful after I had made extended and rather difficult preparations, as follows:

We know from former experiments of M. Sachs (1893) that the degree of contraction of the pupil caused by a colored light, the "*motor irritative value*" of a colored light, depends on the *strength of luminosity* in which the colored light is seen. Until now we lacked a practical method of comparing the changing size of the human pupil and the varying reactions to light in the lower animals. Here you see an apparatus[2] which I constructed for this purpose and which does excellent service also in examining physiological and pathological changes in the human pupil. Of this use of the instrument I shall speak elsewhere in detail. At present it shall be described only in so far as it serves in the solution of the problems in comparative physiology now before us. With the aid of a proper system of lenses, and placed at a certain distance from it, a Nernst lamp illumines very strongly and evenly a circular space. In front of the first lens there is a movable double frame which by a lever arrangement enables one to light this circular space first by a physically exactly determined colored glass light, and immediately thereafter, without intermediate lighting, by a mensurable variable light of almost colorless gray, for comparison. The change in the strength of light in the gray field is caused by the sliding in opposite directions of two acute-angled prisms of gray glass. For every position of the latter, the amount of light which penetrates it from the Nernst lamp is determined; this amount will be expressed in the following table in percentages of the strength of the Nernst light. With this apparatus, which can be used for many purposes, I have made a large number of measurements; if I give only a brief summary of these, please do not conclude a correspondingly brief period of labor on this subject; the table below is alone the result of over 1,000 separate measurements.

MOTOR IRRITANT VALUES OF COLORED-GLASS LIGHTS

The numbers give the amount of light allowed to fall through the gray prisms in percentages of the whole amount striking these, the motor equation determining the former amount.

	Normal human being	Relatively color-blind (blind for red and green, but seeing blue)	Totally color-blind	Dove	Night bird	Sepia	Bees	Centrostephanus	Psammobia
Red	9-11	1.5-2.2	<0.6	7.3-9.3	0.9-1.1	<0.6	<0.6	<0.8	<1.0
Blue	1.5-2.5	2-3	9.9-11.8	0.8-0.9	7.4-8.8	9.3-11.1	8.3-11.1	11.1-14.8	8.3-14.8

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[2] This apparatus, "Differential Pupilloscope," is manufactured by C. Zeiss.

I began with measurements of the normal human eye in order to determine the average pupillomotor irritant value of the various colored lights. Further measurements of relatively blue-seeing, red-green blind (so-called red-blind), showed, as may be seen in the table, that a very slight irritant value of red, and a hardly perceptible variation from the normal motor-irritant value of blue, are characteristic of this disturbance of the sense of sight. For the sake of brevity I shall limit myself in the following to the discussion of the red and blue values, these being of the greatest importance to us. In two cases of totally color-blind which I have repeatedly examined, red proved to have a very slight motor-reactive value (<0.6), blue, a comparatively high value of 9-11.8% (as compared to 1.5-2.5% in the normal eye). These are the three principal kinds of pupil reactions which occur among normal and color-blind human beings and with these we must compare the motor reactive values found among the different animals.

For the day bird, the sensitive value of red is like our own; this corresponds to the fact which I had already discovered by another method, that day birds in most cases see red lights nearly or quite as we see them. The relatively small values of blue,—they are the smallest which I have met with in the animal series—correspond to another fact which I had discovered, namely, that day birds in consequence of red and yellow oil globules located in front of the light receiving apparatus, are relatively blue blind.

With the help of the apparatus I was enabled, among other things, to answer the following question, which I raised some time ago. The beautiful blue of the feathers of many birds is interpreted by almost all zoologists as decorative color for the attraction of the other sex: this interpretation assumes that these birds see blue as we see it, that therefore the oil drops do not exist. For if these drops are found in the eyes of these birds as they are found in the hen and the dove, then a blue which seems to us gorgeous must look to them blue-gray or colorless gray. So far I have had no opportunity to examine such birds with the spectrum according to the method described; but a short time ago I examined the movements of the pupil of the Butterfly-finch (*Mariposa phoenicotis*) with the new apparatus; the motor values are the same as for chicken and dove;

and herewith it is proved that the beautiful blue on breast and tail of this bird cannot be for adornment.

Among the night birds I found the motor values like those of the color blind human eye, a fact which corresponds to the superior number of rods and cones in the retina of these birds. The relatively slight differences are sufficiently explained by the fact that in the retina of the night birds, the cones are not entirely lacking as many assume; indeed, I have repeatedly been able to count in such retinas one to two million cones, with slightly colored oil balls.

Among the invertebrates, examination with the new apparatus of the movements of the pupils of Cephalopods, which are particularly well suited to the measuring experiments, shows as you see striking conformity to the irritative values for the totally color-blind human eye. By the use of other methods also, I have been able to show that these invertebrates are totally color-blind. I cannot here dwell on these new experiments.

A glance at the table will show you further that the motor-sensitiveness of bees to colored lights, of mollusks (*Psammobia*) and of sea urchins (*Centrostephanus*) is almost identical with that of a color-blind man, whereas it differs characteristically from that of red-blind eyes. The reaction of bees I need not mention again, as the bees as well as fish and crabs may easily be proved totally color-blind by other methods which I have developed. The continually repeated mistaken assertions of a few zoologists, from which a color sense in these animals is supposed to be deducible, need no new refutation after the above measurements are studied by anyone at all familiar with the subject.

The advantages of the new methods of research which I have here briefly indicated consist essentially in the following points: All the light reactions which I have hitherto carefully investigated in animals, the contraction of the pupils in birds and invertebrates, the swimming of fish and crabs and the flying of bees toward the light, the phenomena of retraction in *Serpula* and *Psammobia*, the rotations of the little clubs in the *Centrostephanus*, etc., all these manifold movements which are caused by increasing or lessening the light, we are able by the help of our apparatus to measure with the identical, physically exactly determined colored lights, and to express their motor-sensitive values in terms of one and the same measurable variable light with which each colored light is compared. Besides this, we are now in a position to bring all these reactions of animals in relation to the motor-sensitive values which the same colored lights have for the pupil of the normal, the red-blind, and the totally color-blind human eye.

That it would be possible to carry out such exact measurements by this new process, I myself could not foresee at the beginning of these tests; as the results obtained coincide in every detail with those of my former widely differing experiments, they prove most satisfactorily the accuracy of the statements I have previously made about the sight qualities of animals.

IV

The long well-known fact that, on plants, red lights have comparatively slight, blue, on the contrary, strong heliotropic effect, that therefore in this respect there exists a certain similarity between the effect of colored lights on plants and on animals, gave J. Loeb occasion to accept the "Identity of animal and plant heliotropism." Some time ago, referring to older experiments made by Wiesner and to more recent ones by Blaauw, I had expressed doubts of this theory; as in spite of this, Loeb's followers have again energetically taken up the defence of the identity of the two tropisms, it seemed to me advisable to attack this interesting question with new methods. In order to settle it so that every possible objection should be met, both reactions must be studied under identical conditions, with the same colored lights, and especially in quantitative experiments, the same light for measuring must be used for both.

These conditions were fulfilled by the following procedure. Etiolated seedlings of various kinds, in long narrow boxes, were exposed on one side to the rays of a suitable Nernst-light spectrum and simultaneously from the opposite side, to the light used for measurement and comparison, the latter being variable, an electric light placed in a tunnel adapted to the purpose. Its strength I varied partly by changing its position as required, to distances nearer to or farther from the plants, and partly by means of an episkotister. This method proceeds in the same lines as those developed in my experiments with *Artemia* and other animals which shun the light. Starting from a medium distance found by preliminary trials, after a very few hours we find the plants in red, yellow and green bent far over towards the measuring light, those in green, blue and a part of violet, towards the spectrum, those in the outer edge of violet and ultra-violet again bent toward the measuring light. Through this experiment we have found two lights in the spectrum whose heliotropic strength is equal to that of the composite light. The circumstance that the plants bend over on each side of these two colors in opposite directions make a comparatively exact spectroscopic determination of their respective wave lengths possible. By repeating such experiments, taking different distances of the lamp from the plants, I obtained each time two new points for the construction of curves. You see here the curve of the motor irritative values of the different lights of the spectrum for the invertebrates, next to it the curve of some among the plants (*Brassica napus*) which I have observed and you can see from these that there can be no question of identity between the two results; the curve for animals has its maximum in yellow-green, with a wave length of about 526$\mu\mu$, that for *Brassica napus* has its maximum in blue or in the beginning of violet, with a wave length of about 475$\mu\mu$! In yellowish-green, where we find the maximum for animals, the heliotropic effect on the plants has already reached nearly its minimum.

A second method for the investigation of certain questions occupying my attention, I worked out in this way: I have already shown that one can obtain beautiful and convincing results if a reservoir is lighted by rays reflected from colored paper at both ends, and direct light from the window is shut off by placing shades as required. Animals seeking the light, without exception hasten to that end which is lightest in the opinion of a color-blind individual quite irrespective of the way in which normal sight interprets the values. The heliotropic movements of plants have hitherto been observed only when caused by light from the spectrum or through colored glasses; it had never been attempted to find out whether heliotropic movements appear also when light from such reflecting surfaces alone is used. After I had found in a few introductory experiments that such is in fact the case to a quite surprising degree, I used this method for the solution of the problem before us. It is one easily adapted to the use of the interested layman.

If the tropisms were identical, the plants placed between the colored papers should behave in relation to these in exactly the same manner as animals under like conditions. If, however, the heliotropism of plants differs from that of animals as much as the curves indicate, then, if we carefully choose a green surface and a blue, place animals and plants between the two, the former will go to the green side and the plants will bend toward the blue in exactly opposite directions. This behavior is indeed quite marked as you see by the samples set before you. The plants bend over to the blue often in one to two hours after being placed in position.

I have taken the liberty of briefly introducing to you two new methods for the investigation of the heliotropism of plants, because I believe they may do good service in botanical experiments and elsewhere, especially in quantitative experiments, and because particularly the second method may easily be handled by amateurs, and gives marked results, besides being well suited to use in the lecture room. As to the pertinent scientific questions, these I have touched upon today only in so far as the often repeated assertions of Loeb, that animal and plant heliotropism is identical, required a final refutation.

V

In conclusion, let me add a word on my discoveries about the sight qualities of fish and invertebrates. Zoologists and botanists have again and again declared they cannot acknowledge my " theories " (as they call them) because they stand in too harsh contradiction to the prevailing doctrines. The truth of the matter is, that I have never set up any theory whatever, but have made known only facts which every conscientious observer may easily verify for himself. What Sprengel promulgated in 1793, and has been taught ever since about the connection between the coloring of flowers and the visits of insects, was a theory. This theory is now finally done away with, for it is built upon demonstrably wrong surmises as to the sight qualities of bees. Plant biology, for a hundred years and more under the ban of this doctrine, which even Darwin believed to be true, will now needs turn to the task of ascertaining the real meaning of the splendor of color in blossoms.

METHODS OF EXHIBITING REACTIVE TENDENCIES CHARACTERISTIC OF ONTOGENETIC AND PHYLOGENETIC STAGES

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Methods which have contributed importantly to our knowledge of the ontogeny and phylogeny of reactive tendencies, and more especially to those types of adaptive behavior which we call ideational, are few and unsatisfactory. Only recently have experimental devices and procedures been suggested which are alike suited to reveal the reactive tendencies of ontogenesis and phylogenesis and to stimulate interest in genetic description of behavior.

Following a brief historical sketch, I shall describe an apparatus by means of which three of the most recent and promising of our behavioristic methods may be used.

From the birth of interest in the problems of psychogenesis, about the middle of the last century, until the end of the century, no scientific means of approaching the problems of ideational behavior[1] were developed. Romanes, Brehm, Morgan, and their psychological contemporaries who happened to be interested in evolutionary or genetic problems worked either from anecdotal materials or from observations gathered by the use of crude and unstandardized methods which may fairly be characterized as wholly unsuited to scientific inquiry. We regard their contributions to genetic psychology as suggestive of possibilities of research or as defining problems rather than as important additions to our knowledge of fact.

With the appearance of Thorndike's mental initiative, the situation radically changed, for the puzzle-box or problem method came into existence and began to be used systematically as a means of testing for various types of behavior. Thorndike himself devised various forms of apparatus and problem, while at the same time making them contribute most stirringly to our knowledge of the psychology of the chick, cat, dog, and monkey. Kinnaman, Small, Porter, Watson, and a host of other American and European experimentalists followed Thorndike's lead in the application of experimental devices to the analysis of problem-solving behavior.

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[1] I shall designate as ideational behavior those forms of adaptive response which in objective characteristics are identical with, or strikingly resemble, what we appropriately and with common consent call ideational behavior in man.

It may not be amiss to point out that the puzzle-box method, although an important advance scientifically over the casually or inexactly arranged situations of the earlier period—not to mention the anecdote—does not adequately fulfill the requirements of comparative and statistical method. True, it has possibilities of adaptation or improvement in these respects which have never been realized, but the fact is that mostly the data of response to a puzzle-box problem or situation are so meager and inexact as to be of scant value for purposes of comparison or statistical treatment. Comparative and genetic psychology alike demand methods which shall yield precise, varied, and comparable data of reaction from measurements of various stages, types, and conditions of organization.

L. W. Cole departed from the well-worn path which Thorndike had earlier broken, in originating the serial stimulus method of testing for imaginal or ideational behavior. This method, also, was ill-adapted to statistical needs, and like the earlier procedures, yielded only roughly comparable data. As thus far used, it is an indicator of problems rather than a scientifically exact instrument for solving them or of obtaining detailed descriptions of behavior. It has already served an important end in breaking up the monotonous succession of problem-box studies.

Simultaneously with Cole's work on raccoons, which really revived interest in animal ideation, Hamilton, from a very different direction, attacked the general problem of reactive tendencies. As a psychiatrist, he had become deeply interested in applying the comparative method to the problems of psychiatry and in bringing the facts of animal psychology and genetic psychology to bear upon the practical problems of mental disease and defect. His first experimental attempt was a study of reactive tendencies in the dog. Over a period of ten years, he has gradually perfected his method, the while applying it to various ontogenetic stages in man, cat, dog, and monkey, to defective and deranged human adults, and to many and diverse types of animal.

The Hamilton method, which, in the opinion of the writer, is equal in importance to any method of studying behavior yet proposed, has been almost wholly neglected by comparative psychologists and its results are very imperfectly known.

While Cole and Hamilton were busy with their new methods, Carr and Hunter[2] were perfecting, in the study of the white rat, what has appropriately been termed the method of delayed reaction. It is a simple and ingenious way of testing for ideation. Like Hamilton's, Hunter's contribution to our science is important methodologically as well as for its factual materials. But whereas Hamilton's method of quadruple choices is suited to reveal reactive tendencies and to exhibit their genetic relations, Hunter's serves primarily as a test of the ability of an organism to respond to a situation from which the significant feature (stimulus) has vanished.

For purposes apparently foreign to the interests of both Hamilton and Hunter, the writer a few years ago devised yet another method of studying ideational and other reactive tendencies. It has been called the method of multiple choices. It was planned as a means of gathering strictly comparable data of reaction from diverse types of organism, stages of development, and conditions of normality or abnormality. It was the writer's hope and conviction that most varied scientific materials should be assembled systematically in the interest of genetic description. The method is therefore appropriate to human psychology and to infrahuman, to child psychology and to psychopathology.

To sum up:—for reasons which are obvious to every careful student of behavioristic method and result, Hamilton's method of quadruple choices is a preëminently valuable means of displaying reactive tendencies; Hunter's is an uniquely serviceable test of ability to respond appropriately to controllable absent stimuli; and the writer's is a promising mode of evoking varied types of response and of reactive tendency for purposes of classification and more detailed analysis.

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[2] The method is hereafter referred to as Hunter's because he alone has published concerning it.

The three methods differ so much in value, or rather in their special kinds of serviceableness, that they may not be directly compared. All are useful in the study of ideational and other highly adaptive forms of behavior, but each has certain peculiar advantages, whatever the ideational problem in question. For this reason, chiefly, it has seemed to the writer important, as a matter of economy and efficiency of research, to devise a form of apparatus which should enable the investigator to use at will any one of the three methods.

It has not been especially difficult to plan such an apparatus, for the writer has had opportunity to use, and to see used, each method, and has had full advantage of the published results of Hamilton and Hunter, as well as personal contact with them. It may be convenient to refer to the device now to be described as the convertible ideational or reactive tendency apparatus. It is called an ideation apparatus, not because its usefulness is limited to the study of the function of the idea, but because it was originally devised as a means of discovering those types of behavior which are either definitely ideational or closely akin thereto. Objectivists who are offended by the term ideation may substitute reactive tendency or some other equivalent term.

The three methods for which this apparatus may be employed are presented, not as the final word in the study of complex behavior, but rather as the first words concerning a new approach to genetic problems.

DESCRIPTION OF APPARATUS

The apparatus consists (1) of twelve identical boxes, each with an entrance door and an exit door that can be raised or lowered by the experimenter from his observation stand; (2) a reaction chamber in which the subject responds, as may be, to a definite experimental situation, which may be described as a " setting " of the various mechanisms (this setting differs for the three methods, and also from trial to trial in the Yerkes' method); (3) a release box in which the subject is confined between trials and from which it is admitted, at the proper moment, to the reaction chamber; (4) alleys for the passage of the subject from the rear of the reaction mechanisms or boxes to the release box; (5) twelve reward mechanisms, one for each box; (6) a keyboard, or series of levers, (depending upon the size of the apparatus) connected by means of cords or wires with the various entrance and exit doors of the apparatus, and so arranged as to enable the experimenter to unlock and open or to close and lock any given door by a simple movement of a key or lever; (7) a protected incandescent lamp in each of the boxes, with the necessary switch and timing mechanisms for its satisfactory use in connection with the Hunter method of delayed reaction (lamps need not be installed in the twelve boxes, but only in those which are to be used for the delayed reaction method).

This apparatus may be built in three sizes: small, medium, and large.

The small apparatus is suitable for experiments with such organisms as the toad, frog, lizard, tortoise, mouse, rat, sparrow, canary, and other like-sized amphibians, reptiles, birds, or mammals. The medium-sized apparatus is suited for experiments with the tortoise (large), snake, dove, crow, domestic fowl, cat, small dog, raccoon, rabbit, squirrel, marmoset, and other medium-sized reptiles, birds, or mammals. The large apparatus may be used for various types of large-sized lower vertebrates, and for such mammals as the cat (large), dog, pig, goat, sheep, bear, monkey, ape, and man.

The several figures indicate the general plan of the apparatus and certain of the most important points of construction.

Each reaction box, according to figures 1 and 3, and also according to the measurements of table 1, occupies five degrees of arc. The width of the box is therefore determined by its distance from the center X (figures 1 and 3). By making the boxes intercept six degrees instead of five, the advantage can be gained of shorter distances between release door and entrance door, but there results the serious disadvantage that the apparatus is so spread out as to demand a considerable eye movement for inspection of the twelve reaction boxes. There is the further disadvantage, in the wider angle, that the large apparatus requires for its installation a floor area of nearly thirty-six by thirty-six feet. For these and other reasons, it has seemed desirable to make use of the five degree angle in the designing of this convertible apparatus.

The alleys are, in each size of apparatus and throughout their lengths, the same width inside as the reaction boxes are outside.

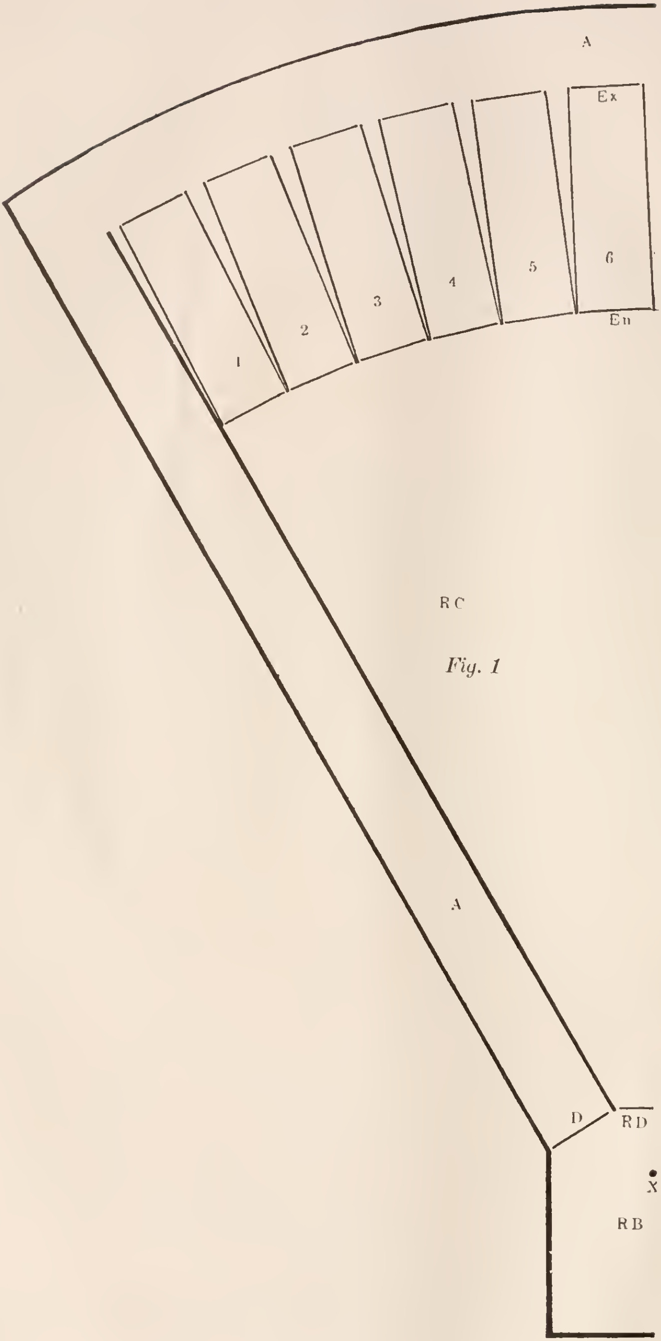

FIGURE 1.—Left half of medium sized reactive tendency apparatus. (1) 1-6, reaction mechanisms or boxes; En, entrance door; Ex, exit door; (2) RC, reaction chamber; (3) RB, release box; RD, door between release box and reaction chamber; (4) A, A, alley from reaction boxes to release box; D, door between alley A and release box; X, center of circle on arc of which reaction boxes are placed.

The plan of the medium sized apparatus appears as figure 1, and in figure 2 there is shown an enlargement of one of the reaction boxes, with the arrangement of sliding entrance and exit doors and the concealed reward mechanism. Figure 3 represents the three sizes of apparatus in their relations. These must, of course, be built separately and be independent of one another.

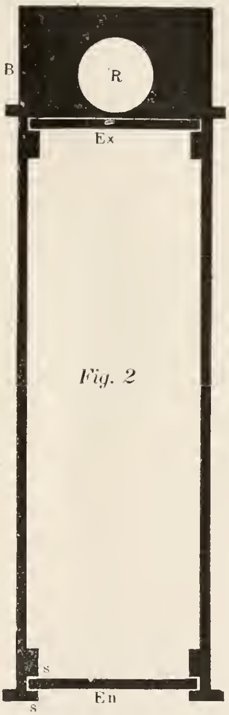

FIGURE 2.—Ground plan of reaction box. En, entrance door; Ex, exit door; s, s, wooden guides for sliding door; B, wooden block for food cup; R, food cup.

The small apparatus should be made of quarter inch white wood (poplar), red wood, or pine, according to locality, and covered with netting made of No. 20 wire, three meshes to the inch. The medium sized apparatus should be made of half inch stock, and the wire netting used as a covering, or for other necessary purposes in connection with it, should be No. 17 wire, two meshes to the inch. The large apparatus should be made of seven-eighths inch stock, and the accompanying wire netting should be made of No. 12 wire, one mesh to the inch.

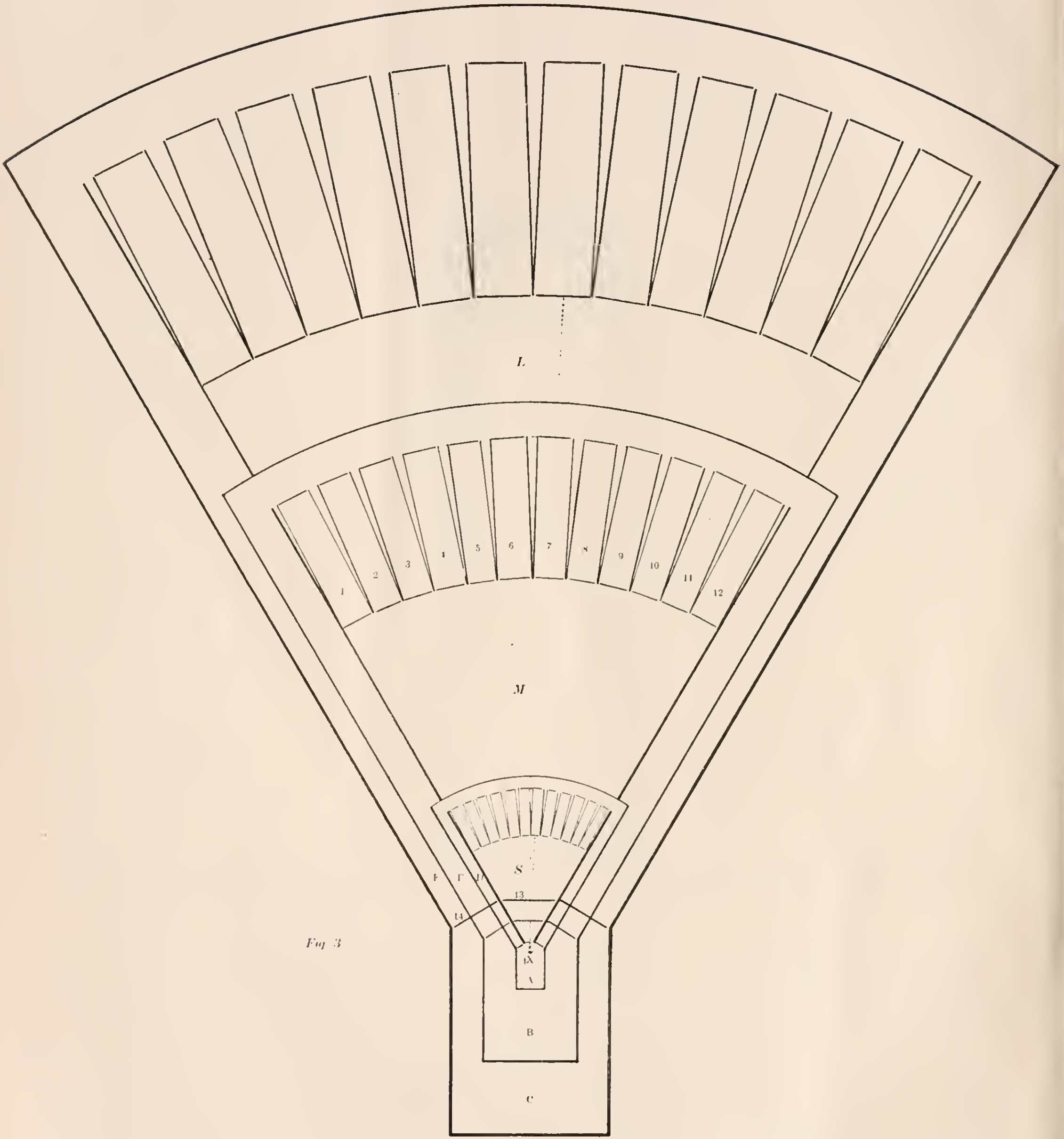

FIGURE 3.—General plan for three sizes of reactive tendency apparatus. S, small apparatus; M, medium apparatus; L, large apparatus. X, center of circles on arcs of which reaction boxes and outer alley walls are placed; A, release box for small apparatus; B, release box for medium apparatus; C, release box for large apparatus; D, E, F, alleys for small, medium, and large apparatus, respectively; 13, release door (the release doors for the three sizes of apparatus are shown); 14, door between release box C and alley F.

All stock should be planed on both sides, and the apparatus should be given two or three coats of dark gray paint, if it is to be exposed to the weather. If, instead, it is to be used indoors, it should be painted white or gray, according to the degree of illumination of the experiment room.

The walls of the reaction chamber should be made of wire netting of the weight indicated above. The outer walls of the alleys may be made of wood or wire netting. The release box should be built of wood except for the wire netting cover and door. The entrance and exit doors should be made of wood.[3]

In table 1 are presented the chief dimensions for the three sizes of apparatus under consideration.

TABLE 1

Principal Dimensions in Centimeters or Inches of Convertible Reactive Tendency Apparatus

Measurements	Dimensions for Small	Dimensions for Medium	Dimensions for Large
Of reaction boxes			
Width outside........	10 cm.	30 cm.	60 cm.
Width inside (minimum)	7.5 cm.	25 cm.	51 cm.
Length outside.......	30 cm.	60 cm.	140 cm.
Length inside.........	29– cm.	58– cm.	135– cm.
Depth outside........	20 cm.	40 cm.	200 cm.
Depth inside.........	19+ cm.	38+ cm.	198– cm.
Of entrance and exit doors			
Width...............	8.4 cm.	27 cm.	54 cm.
Length..............	20 cm.	40 cm.	200 cm.
Of release box			
Width...............	33+ cm.	99+ cm.	198+ cm.
Length..............	30 cm.	60 cm.	140 cm.
Depth...............	20 cm.	40 cm.	200 cm.
Of release box doors			
Width...............	10 cm.	30 cm.	60 cm.
Length..............	20 cm.	40 cm.	200 cm.

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[3] For details see *Behavior Monographs*, vol. 3, no. 1, p. 14.

Measurements	Dimensions for Small	Dimensions for Medium	Dimensions for Large
Of alleys			
Width inside	10 cm.	30 cm.	60 cm.
Depth	20 cm.	40 cm.	200 cm.
Distance from center X to entrance doors	114.5 cm.	343.6 cm.	687.1 cm.
Distance from release door to entrance doors	105.9 cm.	317.6 cm.	635.1 cm.
Of strips for doors to slide in			
Thickness	1/4 in.	1/2 in.	7/8 in.
Width	2 cm.	3.5 cm.	6.5 cm.
Length	20 cm.	40 cm.	200 cm.
Block for reward mechanism			
Width	6 cm.	10 cm.	15 cm.
Length	10 cm.	30 cm.	60 cm.
Depth	2 cm.	4 cm.	6 cm.
Hole in block			
Diameter	4+ cm.	6+ cm.	7+ cm.
Food cup			
Diameter at top	4 cm.	6 cm.	7 cm.
Depth	2 cm.	4 cm.	6 cm.
Cover for food cup			
Width	7 cm.	20 cm.	30 cm.
Length	8 (2+6)	14 (4+10)	25 (10+15)
Space necessary for apparatus in use			
Width	10 ft.	20 ft.	30 ft.
Length	12 ft.	20 ft.	36 ft.

Certain suggestions concerning details of construction are of practical importance. It is desirable, for the sake of uniformity, to supply each box with a floor. This floor should be cut shorter than the sides of the box so that the entrance and exit doors may drop past it, thus discouraging attempts of subjects to raise the doors. Or, if the floor is cut full length, a strip nailed across the box just inside of the exit door will serve the same purpose while giving support to the floor.

Each box should have a wire netting cover on top.

All doors should slide vertically, upward, in wooden ways. These are conveniently made by nailing strips of wood to the side walls of the box. The strips serve the additional purpose of supporting the side walls. The outside strip may either be nailed to the end of the side wall or along the side. If nailed to the end, it serves as the outside strip for adjacent doors and thus reduces the amount of labor. In figure 2, the outside strip for the entrance door is shown as nailed to the end of the side wall. The writer prefers this method of construction.

The reward receptacle, or mechanism, must be so constructed as to be concealed when the exit doors are down and fully exposed when they are raised. It may be simply and conveniently constructed by nailing outside the rear end of each box a block of wood, of the dimensions suggested in the table, in the center of which there is a hole large enough to receive a metal food cup. Aluminum is preferable as material for the food cup, and desirable dimensions for the various sizes of apparatus are suggested in table 1. In the proper position on the outside of the exit door, there should be screwed a metal plate, bent at right angles in such wise as to cover completely and tightly the food cup when the exit door is down. This is shown in figure 4.

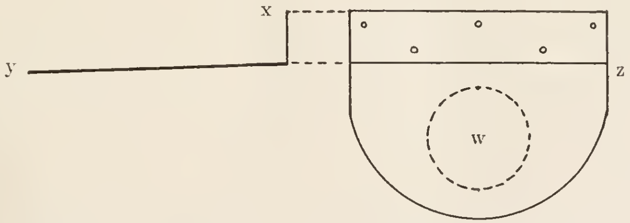

FIGURE 4.—Metal cover for food cup. w, position of food cup under cover; z, point at which cover is bent nearly at right angles; x, portion of cover which is attached to exit door by means of wood screws, holes for which are indicated; y, portion of cover which hides food cup.

The dimensions for this cover or cap for the food cup, also, are indicated in table 1. For the small apparatus, heavy tin is a satisfactory material for this cover; for the medium apparatus, light galvanized iron suffices; and for the large apparatus, it is necessary to use galvanized iron which is so thick that the large apes cannot readily bend the cover out of shape. The thickness should be about 1/16 inch.

For most animals there is no necessity of locking the doors of the apparatus, but when it is to be used with monkeys or anthropoid apes, it is absolutely necessary that the experimenter be able to securely lock any one or all of the sliding doors. It is therefore essential to equip the large sized apparatus with locks to be operated in connection with the mechanisms which raise and lower the doors. Each door should lock automatically when lowered and unlock when the raising mechanism is operated.

Just behind and a trifle above the release box, an observer's stand or record table should be constructed, separated by a screen from the apparatus so that the animal shall not be able to see the observer. On this table there should be placed a keyboard, or lever device, by means of which any one of the twenty-six working doors[4] of the apparatus may be raised or lowered quickly and quietly.

For the small apparatus the various doors may be controlled readily by means of a light cord, which runs from a screw eye in the top of each door, through appropriately placed pulleys, to a hinged lever key which the observer operates. This key should be so arranged that when it stands in approximately vertical position the entrance door is closed. When it is placed in the horizontal position, the entrance door is open. A cord from the exit door, carried similarly by pulleys, should be so placed that it may be attached readily by means of hook and ring, or ball and slot, to this key, so that if, when a given entrance door is lowered, the experimenter desires to raise, simultaneously, the exit door of the same box, the pushing of the key to the vertical position will effect the appropriate movement of each door, that is, will simultaneously lower the given entrance door and raise the given exit door. The distance to which the entrance door is raised may be altered by changing the point of attachment of the cord to the key. This simple hinged key and cord device renders necessary the use of only fourteen keys for the operating of twenty-six doors, but the scheme is feasible only so long as the doors in question are light enough to be readily moved by means of a fairly small lever key. The accompanying diagram, figure 5, indicates the relations of parts, as described above.

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[4] If both return alleys are used there are twenty-seven doors instead of twenty-six to operate.

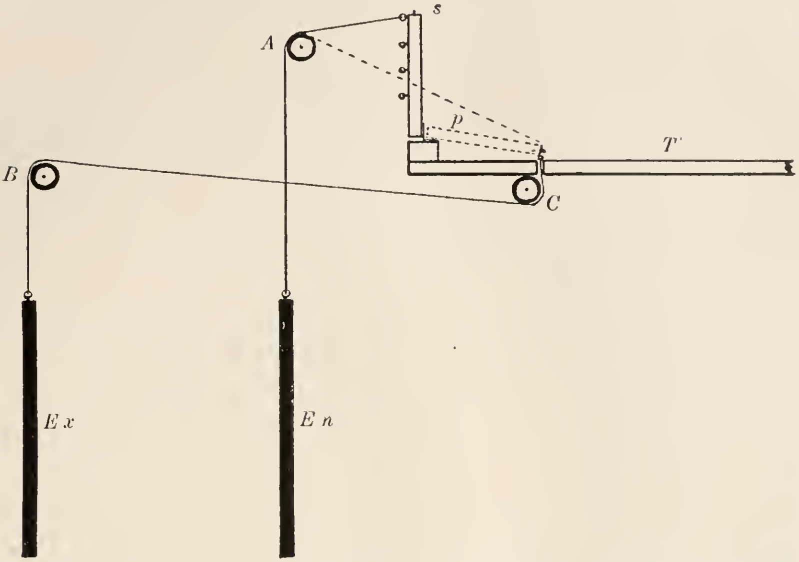

FIGURE 5.—Diagram of lever-key mechanism for raising and lowering doors. En, entrance door; Ex, exit door; T, observer's table; s, hinged lever key in vertical position; p, same, in horizontal position; A, pulley for cord between entrance door and lever key; B, pulley for cord between exit door and lever key; C, second pulley for cord from exit door.

For the medium sized apparatus also, the lever key mechanism is feasible, but it requires considerably more space and much greater effort on the part of the experimenter. A substitute for it is the weighted cord mechanism.[5] A cord with appropriate carrying pulleys is provided for each door, and to the end of the cord, which drops in front of the experimenter's table and within easy reach, is attached an iron or lead weight which is just sufficient to hold the door in position after it has been raised by the experimenter. If the weight is too heavy, the door will tend to rise at inappropriate times; if too light, it will not stay in position after being raised. This device has the defect of varying in reliability with humidity and temperature, since the door will slide more or less easily in accordance with these varying conditions. The lever mechanism is preferable, since it can be relied upon to place and hold the doors in a constant position.

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[5] Described in previous papers on the multiple-choice method. A study of the behavior of the pig *Sus Scrofa* by the multiple-choice method, *Journal of Animal Behavior*, 1915, **5**, p. 188. The mental life of monkeys and apes: a study of ideational behavior, *Behavior Monographs*, 1916, **3**, p. 14.

For the large apparatus, it is extremely desirable to devise some type of lever mechanism which shall be easily manipulated, reliable, and inexpensive. All of the mechanisms thus far proposed are either too cumbersome or too expensive to be feasible, but it is hoped that shortly a method may be discovered by which the experimenter may conveniently and accurately control the various doors by means of levers, the maximum excursion of which shall not exceed eighteen inches. Since the various doors must be raised a maximum of seventy-two inches, it will probably be necessary to introduce one or more forms of multiplying device. Already an automatic locking device, to be operated in connection with the proposed system of levers, has been designed.

In the absence of a satisfactory scheme for the use of levers, weighted cords and locks, which are operated independently, may be employed. But this system of control mechanism, as has been stated above, is both unreliable and troublesome to operate because of the numerousness of the parts. There must be a separate weighted cord for each of the twenty-six doors and a separate lock mechanism for each of the twelve boxes, entrance and exit door in each case being controlled by the same lock.

USE OF APPARATUS

The use of the convertible reactive tendency apparatus in connection with each of the three methods in question will now be described. For all of the methods alike, rewards and punishments may be used as inducements to effort. As rewards, food presented in the food cups, or for children small presents similarly presented, serve well. In certain exceptional instances, it may prove desirable to present the reward for a successful choice, not in the food cup of the correct box, but instead at the entrance to the release box. As punishment, it has proved feasible to use confinement in incorrect boxes. It seems probable that for certain organisms the electric shock may prove useful.

Hamilton Method

For use with the Hamilton method of quadruple choices, the following procedure is suggested. This method involves the use of only four reaction mechanisms. Boxes 5, 6, 7 and 8 may therefore be used, the fact that they are to be reacted to being indicated by their openness, the entrance doors being raised in case of each trial. Since the entrance doors of all other boxes should remain closed and locked, there would be no persistent tendency on the part of most organisms to attempt to enter other than the four boxes referred to. For some purposes, it may prove even more satisfactory to use boxes 2, 5, 8 and 11.

Incorrect choices would not be rewarded, and as seemed desirable the subject could be punished for such choices by being confined in the boxes for a stated period. A correct choice, no matter what the particular form of the problem, would naturally be rewarded by the presentation of food in the food cup.

Various problems, in addition to that originally suggested by Hamilton, may be presented by this method. The following will suggest the range of possibilities: (1) An insoluble problem, such as Hamilton used, the several boxes serving as correct boxes in irregular order, but the same one never twice in succession and each the same number of times in every hundred trials (this problem is practically insoluble by even the most intelligent organism); (2) the systematic use, as correct box, of each in turn from the left end to the right end, that is, 5, 6, 7, 8, or in case of the other group of boxes, 2, 5, 8, 11, this succession being repeated indefinitely; (3) box at left end, box at right end, box next to left end, box next to right end, the same being repeated indefinitely. From these suggestions, it is evident that various degrees of complexity of order and relationship might be utilized to elicit reactive tendencies and to display problem solving ability of different sorts.

The apparatus demands no special modification or adaptation for use in connection with the Hamilton method. Further details are unnecessary in view of the fact that Hamilton has already published a fairly complete description of method and apparatus,[6] and has in press a still more elaborate account of procedure and results.[7]

Hunter Method

For the method of delayed reaction the apparatus demands certain special appliances which, however, do not have to be removed when either the Hamilton or the Yerkes method is in use. The special equipment consists of a concealed incandescent electric lamp for the illumination of each box and an electric signal and timing mechanism for the operation of the lamps and the door between the release box and the reaction chamber.

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[6] Hamilton, G. V. A study of trial and error reactions in mammals. *Journal of Animal Behavior*, 1911, **1**, pp. 33-66.

[7] *Behavior Monographs*, 1917, **3**, no. 13.

The method of delayed reaction may be used with various groups of doors, according to the grade of difficultness of response desired. Thus, as the simplest situation, boxes 6 and 8 may be used. In this case, the entrance doors of both boxes should be raised in preparation for a trial. The doors of the other boxes should remain closed. In accordance with a prearranged plan, either the one or the other box would be indicated, by momentary illumination, as the box to be chosen.

For the second grade of difficultness, boxes 5, 6, 7 and 8 might be used, each of them having the necessary equipment and connections for use as the correct box; for grade three, boxes 2, 5, 8 and 11; for grade four, boxes 1, 3, 5, 7, 9 and 11; and for grade five, all of the twelve boxes might be subject to use, that is, the entrance door of every box should be open and the subject should be required to choose that one of the twelve which has previously been illuminated.

The satisfactory use of this method necessitates not only the presence of a lamp, but the installation of a mechanism which shall control several important factors in the situation. The experimenter, by pressing a simple key, should close a circuit which at once illuminates a certain box (the particular box to be determined by the setting of a switch), and at the same time starts a timing mechanism. This mechanism should, after an interval, with a range of 1 to 10 seconds, open the lighting circuit, thus cutting off the illumination of the correct box; and after an interval of 0 to 60 seconds it should cause the door of the release box to open so that the animal may enter the reaction chamber. For intervals longer than 60 seconds, it seems best to have the experimenter determine the delay by means of a stop watch and operate the door of the release box by hand.

There is no obvious reason why this twelve mechanism reactive tendency apparatus should not be used in wholly satisfactory fashion for the study of delayed reactions. The additional electrical equipment should in no wise interfere with the other uses of the apparatus and that portion of it which controls the release box door might be made to serve the experimenter in connection with all of the methods.

Yerkes Method

For use by the method of multiple choices, the apparatus demands neither modification nor special adaptation. The chief features of the method have already been described several times, and it is needless here to do more than formulate a set of problems with wider range of difficultness than those heretofore used in reported experiments on lower animals. Those proposed problems, ten in number, are presented in brief form below, with a series of ten settings for each. Thus, in case of problem 1, for which the correct mechanism is always box number 5, that is the fifth from the left end of the apparatus, the first setting involves the use of boxes 1 to 6, the second setting, of boxes 3 to 12, and so on. It is understood that, if possible, this series of ten settings (ten trials) shall be presented to a subject once a day until the problem has been solved. If for any reason the series of ten trials cannot be completed on a given day, it should be resumed from the point of interruption on the following day. If more than one series per day can be given, either the ten trials may be divided into two groups of five each or the total series may be repeated.

In each of the series of ten settings, a total of sixty boxes is presented. The average number of boxes open in each trial is, therefore, six. Of these sixty boxes, ten are definable as correct boxes. The probability of correct first choice prior to experience is for any series of ten trials, one to five. In order that this ratio of probable right to wrong first choices shall not be disturbed, it is desirable that the experimenter make use of the proposed settings.

PROPOSED PROBLEMS AND SETTINGS FOR MULTIPLE-CHOICE METHOD

Problem 1. Same box (box 5).
1-6 (5); 3-12 (5); 4-6 (5); 5-9 (5); 2-10 (5);
4-5 (5); 4-10 (5); 3-6 (5); 1-8 (5); 5-10 (5).

Problem 2. First at left end.
6-12 (6); 11-12 (11); 3-11 (3); 1-5 (1); 4-11 (4);
10-12 (10); 5-9 (5); 2-12 (2); 8-11 (8); 7-12 (7).

Problem 3. Middle.
1-7 (4); 10-12 (11); 6-10 (8); 1-11 (6); 1-3 (2);
4-10 (7); 1-9 (5); 9-11 (10); 1-5 (3); 6-12 (9).

Problem 4. Third from right end.
1-6 (4); 5-8 (6); 3-12 (10); 1-3 (1); 7-11 (9);
2-10 (8); 1-7 (5); 3-5 (2); 2-9 (7;) 1-5 (3).

Problem 5. Alternately left end and right end.
8-12 (8); 1-10 (10); 3-8 (3); 6-9 (9); 1-9 (1);
3-5 (5); 7-11 (7); 5-12 (12); 2-8 (2); 4-6 (6).

Problem 6. Progressively from right to left end of apparatus—toward left by ones.
10-12 (12); 6-12 (11); 3-10 (10); 8-12 (9); 8-10 (8);
1-9 (7); 5-8 (6); 4-9 (5); 2-11 (4); 3-7 (3).

Problem 7. One place to left of middle key.
6-12 (8); 3-5 (3); 8-12 (9); 1-9 (4); 2-12 (6);
10-12 (10); 5-11 (7); 1-5 (2); 3-9 (5); 1-3 (1).

Problem 8. Alternately second from right and second from left.
6-12 (11); 2-5 (3); 1-8 (7); 5-9 (6); 1-5 (4);
4-12 (5); 5-10 (9); 9-11 (10); 2-9 (8); 1-5 (2).

Problem 9. To the right of mid-point in even group; or first member of second-half of group.
3-10 (7); 1-4 (3); 2-7 (5) 1-2 (2); 3-12 (11);
8-11 (10); 5-12 (9); 1-10 (6); 5-10 (8) 11-12 (12).

Problem 10. Alternately to left of middle key and to right of it.
1-7 (3); 8-12 (11); 2-10 (5); 10-12 (12); 1-9 (4);
3-9 (7); 1-3 (1); 6-10 (9); 6-12 (8); 3-7 (6).

The various forms of problem serviceable in connection with the different methods and the detailed procedure for each remain to be worked out. The methods have been thoroughly tried out and have already yielded such valuable results that further development and application is obviously desirable. There is no reason why the same apparatus should not henceforth serve for studies of reactive tendencies and ideational behavior by the method of quadruple choices, that of delayed reaction, that of multiple choices, and that of conditioned reflexes.

We experimenters shall doubtless do well to use our devices to the limit of their applicability, seeking no less assiduously new ways of employing existing experimental equipment than we seek to invent new mechanisms.

LIGHT REACTIONS OF THE CRIMSON-SPOTTED NEWT, *DIEMYCTYLUS VIRIDESCENS*

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INTRODUCTION

The following experiments, which are extensive rather than intensive in character, were started with a dozen salamanders obtained in the month of November from the Marine Biological Laboratory at Woods Hole. During the course of the experiments, which extended over a period of more than a year, three of the animals escaped, so that some of the later results were obtained with only nine animals; they were obtained from Woods Hole because of their comparative rarity in the neighborhood of Morgantown when the work was begun. Later, animals were caught in a local pond and these were also used in the experiments.

No change in reaction, except in one possible case, was produced by prolonged residence (for a month or more) in a photographic dark room, though it was noted that all of the animals were of a lighter shade of color when first brought from the dark room.

In all but one or two cases the animals were confined in a rectangular glass aquarium, six inches wide by ten inches long, with two or three inches of water. The water was used chiefly for two reasons: because the newts were very much more active in the water than they were in the empty aquarium, and because the water, of course, acted as a heat-screen and practically eliminated heat as a stimulus.

A few tests were made without water, with no noticeable difference in reaction except speed; the animals responded two or three times as quickly when in water than they did when in the merely moistened aquarium.

Observations made upon animals in an evenly illuminated aquarium seemed to show that they have a certain tendency to collect in groups, in one place or another, without regard to the light stimuli to which they are subjected; this tendency, then, has no apparent bearing upon the following experiments.

After hundreds of observations, extending over a period of many months, upon several lots of animals, several sets of observations were made upon one or two small groups of animals immediately upon bringing them into the laboratory from their native pond. Under these conditions the animals responded either very indefinitely to the same light stimuli, or even in a contrary manner to the animals that had been for some time under observation. This irregularity in what had been considered the normal response was also noticed in a group of animals that had been in the aquarium for a long time and had not been used in the experiment for a considerable period.

It is possible that, after all, the responses of the animals under these abnormal conditions may be quite different from what would be seen under normal conditions in their native habitat.

It is the intention of the author to carry on similar experiments upon this species in the natural environment as soon as a suitable spot can be found. (See Addendum.)

Experiment I.—This experiment was to determine whether Diemyctylus is positively or negatively phototropic towards white light.

Twelve animals were placed in the above-described aquarium of water which was entirely surrounded by black except over half of the top. Ten inches above the surface a 25-watt, 115-volt tungsten lamp was so fixed as to illuminate exactly one-half of the aquarium, the other half, of course, being thrown in dense shadow.

At regular intervals of five minutes the numbers of animals in both light and dark ends were noted. When an animal, at the moment of observation, happened to be partly in light and partly in shadow it was counted for that region in which the greater part of its length lay, though occasionally an animal was so near the exact center that it was not counted on either side.

Table I shows that in 30 observations 95 animals were found in the light and 250 in the dark. These observations were taken on three different days; and after observations 5, 7 and 17 the light and dark ends were suddenly interchanged, thereby throwing the larger proportion of the animals, that had collected in the shadow, into the light. The last five observations were made about two weeks after the first, during which time three of the animals had escaped.

TABLE I

Observation. . .	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Light half.	2	3	2	2	2	0	0	1	2	0	4	2	2	5	2
Dark half.	10	9	10	10	10	12	12	11	10	12	8	10	10	7	10

Observation. . .	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Totals
Light half.	1	2	6	4	5	4	3	5	4	1	4	8	9	5	5	95
Dark half.	11	10	6	8	7	8	9	7	8	11	5	1	0	4	4	250

Another set of observations made under the same conditions, except that only enough water to moisten the bottom of the aquarium was used, gave 141 animals in the light to 243 in the dark region. As noted above, without enough water to swim in the newts are so sluggish that experimentation is not nearly so satisfactory as when they are actively swimming.

It is evident, then, that, at least under the conditions of the experiment, these newts are negatively phototropic.

Experiment II.—Variations of experiment I were tried to determine the effect of temperature upon the phototropic reactions of Diemyctylus.

The first variation was merely to start the observations, made upon eleven animals, with the water at 10° C., the arrangement of aquarium and lights being as in experiment I. Not only was the aquarium surrounded by black, but the experiment was performed in a photographic dark room. Beween the 15th and 16th observations was an interval of two hours, during which time the animals were in the dark. After the 30th observation, when all the animals were in the dark half of the aquarium, the ends were reversed, throwing all the animals into the light half. When the animals, as in this case, were sluggish it would be some time before they would move into the dark again, which would reduce the total preponderance of dark over light. The total figures for 40 observations were 174 in the light end to 278 in the dark, which was about the proportion noted in experiment I when no water was used. At the end of this part of this experiment the temperature of the water had risen about 2° C.

In the second variation of this experiment the aquarium containing the animals was placed out-of-doors for about five hours, until the temperature of the water had fallen to 1° C.; it was then brought into the dark room where the same arrangement for vertical illumination of just half of the aquarium as in experiment I was used. All of the animals at this temperature were numb with cold, and lay motionless on the bottom of the aquarium. One or two were apparently dead and when turned over, ventral side up, made no effort to right themselves. At the beginning of this series of observations six animals were placed in the dark end of the aquarium and five in the light end.

TABLE II[1]

Observations..	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Light half.....	5	5	5	5	5	4	4	4	4	4	4	4	4	4
	s	s	s	s	s	S	S	s	s	s	s	s	s	s
Dark half.....	6	6	6	6	6	7	7	7	7	7	7	7	7	7
	s	s	s	s	s	S	S	S	S	s	s	S	S	S–

Observations..	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Light half.....	6	6	6	7	2	2	1	0	0	0	10	7	4	4
	S	s	s	S	S–	S–	A	..	..	..	S–	A	A	A–
Dark half.....	5	5	5	4	9	9	10	11	11	11	1	4	7	7
	S	S	S	S	S–	S–	S	A–	A–	A	s	S–	S	S

Observations..	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Light half.....	3	0	0	5	5	4	2	2	5	2	3	1	1	1
	A	..	..	S–	a	A–	A–	S	a	A	a	A	A	A
Dark half.....	8	11	11	6	6	7	9	9	6	9	8	10	10	10
	S	S	S	S–	S–	S	A–	S	a	A	A–	A–	A–	A

Observations..	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Light half.....	0	6	4	4	5	3	3	1	5	7	6	6	8	8
	..	A	A–	A	A	S	S–	A–	a	a	a	a	a	a
Dark half.....	11	5	7	7	6	8	8	10	6	4	5	5	3	3
	..	S	A–	s	S	A–	S–	A–	A	A	a	A	a	A

Observations..	57	58	59	60	61	62	63	64	Totals
Light half.....	5	6	2	9	5	9	5	2	259
	a	A	A	A	A	a	a	a	
Dark half......	6	5	9	2	6	2	6	9	446
	A	A	A	A	A	a	a	A	

Observations were begun at intervals of three minutes, but as no change of position had taken place at the end of fifteen minutes the interval between observations was changed to five minutes, from observations 7 to 21, after which it was again made three minutes.

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[1] In this and the following experiments the letters refer to the average activity of the animals at the time of observation—

a = very active; A = less active; A— = still less active.
s = very quiet; S = less quiet; S— = still less quiet.
A— and S— would probably be about the same state of activity.

It will be seen from table II that, for the first 18 observations, lasting about one and one-fourth hours, there was very little change in the position of the animals, which lay almost motionless during that time. At the 18th observation the temperature of the water had risen to only 7° C., and warm water was carefully added until that in the aquarium was raised to 13.5° C.; the animals soon began to become more active, and after twenty minutes (22nd observation) all were collected in the dark half of the aquarium. From the 22nd observation until the end of the experiment observations were made at intervals of three minutes. It will be seen by table II that the light was changed after the 24th observation, throwing all the animals into the light end; after fifteen minutes all the animals had again collected in the dark region.

After the 31st observation, when the water of the aquarium had risen to 15° C., warm water was again added until that in the aquarium was raised to 24° C.; this operation was repeated after the 36th observation and the temperature raised to 33° C. The animals were mostly very active but continued to collect in the dark region, so that after the 43rd observation, when all were in the dark, the ends were reversed, throwing all the animals in the light end.

After the 50th observation, when ten of the eleven animals were in the dark region, enough water was added to raise the temperature to 36.5° C.; this caused the animals to become unusually active, to frequently give a squeaking sound, and to come to the surface for air. After this, it will be noticed from the table, there is no longer a tendency to collect in the dark, possibly a slight tendency in the reverse direction. After the 59th observation water was again added until that in the aquarium was raised to to 38° C. At this temperature the animals acted as just described, but with more vigor. Some of them were so seriously affected that they turned ventral side up and could scarcely right themselves again, and it was evidently impossible to further increase the temperature without endangering the lives of the animals.

It is apparent, therefore, that low temperatures, not far above the freezing point of water, cause these animals to become so sluggish as to be more or less indifferent to differences of light and darkness. As the temperature rises they become active and seek the dark region of the aquarium. When the temperature reaches about 36° C. they become abnormally active and again become indifferent to light and shade differences. At somewhat less than 40° C., about the temperature of human blood, (though they could doubtless be acclimated to higher temperatures) they are seriously affected or possibly killed.

Experiment III.—Another variation of experiment I was to determine whether the animals would seek the dark half of the aquarium when the illumination was from below.

The same aquarium and eleven animals were used as in the preceding experiments, but the light was thrown from below by the same tungsten lamp, placed six inches below the bottom of the aquarium. In all, 60 observations, at three-minute intervals, were made, with a rest of three and one-half hours between the 30th and 31st observations. The temperature of the water was about 27.5° C. and the animals were active throughout the experiment, those in the light being the more active, on the average. The total number of animals counted in the light was 266; those in the dark, 360.

It is evident then, that Diemyctylus tends to come to rest in the dark region of the aquarium when the light comes from below, but that the tendency is not so strong as when the source of light is above the water.

Experiment IV.—This experiment was to determine the reaction of Diemyctylus in relation to the direction of white light.

In this and similar experiments both the region of the aquarium where found and the position of the animal in relation to the direction of the light were noted. It was noticed that when the aquarium, described on page 29, was placed with one end about eight feet from a window, but not in the direct sunlight, on a fairly bright day, a large proportion of the animals stayed in the end of the aquarium towards the light and swam against the glass as though trying to get nearer the window. No actual counts were made in this observation.

TABLE III

Observations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
Facing light	8 A–	8 A–	6 A–	7 S–	7 A	6 A	7 A–	7 A	7 A–	6 A–	5 a	4 A	6 A	9 A–	8 A–	6 a	8 A	6 A	9 A–	6 a	136
Facing dark	3 S	3 S	5 S	4 S	.. ..	5 A–	4 S–	4 S–	4 S	2 S	4 S–	4 S	1 S	2 S	3 S	4 S–	3 S–	4 S–	2 S–	5 S–	68
In light end	7 A	6 A–	4 A–	5 A–	7 A	5 A–	6 A–	8 A–	4 *A*	4 A	5 a	4 A	6 A	7 A–	7 A	7 A	8 A	6 A	7 a	6 a	119
In dark end	4 S	5 S–	7 S	6 S	4 S	6 A–	5 S–	3 S–	7 S–	7 S	6 S–	7 S	5 S	4 S	4 S	4 S–	3 S	5 S	4 S	5 S–	101

Table III shows the results of a series of observations upon the same eleven animals used in the preceding experiments, The aquarium, containing a few inches of water, was entirely surrounded by black except at the end which was towards the window, in this case twenty feet away. The day, while not dark, was overcast, and the light that entered the open end of the aquarium was naturally quite dim. When an animal, at the instant of observation, lay at right angles to the direction of the light it was not counted. It will be seen that exactly twice as many animals faced towards the light as faced away from it, while the number of animals in the half of the aqaurium near the window was not very much greater than the number in the other half. It will be noticed also that, as a rule, the animals facing the light were more active than those facing in the other direction, and that those in the half nearer the light were more active than the others.

This experiment shows that these salamanders are positively phototactic even towards weak daylight.,

Experiment V.—This experiment or series of experiments was to determine the reaction of the animals towards a much more intense white light than the daylight of the preceding experiment. The light here used was the same 25-watt, 115-volt tungsten lamp that was used in experiment I; it was placed six inches from the open end of the aquarium. The aquarium was surrounded except at one end by a black cloth, and the whole apparatus was operated in a photographic dark room. Observations were made at intervals of five minutes. The temperature varied from 16.5° C. to 19° C. Eleven animals were used. At the beginning of the experiment the animals were quiet and equally distributed through the aquarium.

TABLE IV

Observations	1	2	3	4	5	6	7	8	9	10	11	12	13
Facing light	7	10	9	7	10	10	8	10	9	7	8	8	4
	S–	A–	A–	a	A	A	a	A	A	A	A	A	A–
Facing dark	1	1	2	4	1	1	3	1	2	4	3	3	7
	S	S	..	S–	A–	S	S–	S	S–	S–	S–	S	A–
In light end	7	8	7	7	8	8	10	8	7	6	9	5	4
	S–	A–	A	a	A	a	A	a	a	a	a	a	A–
In dark end	4	3	4	4	3	3	1	3	4	5	2	6	7
	S	S–	A–	S–	A–	S–	S	S	S–	S–	S	S	A–

Observations	14	15	16	17	18	19	20	21	22	23	24	25	26
Facing light	6	9	10	7	10	8	8	9	10	8	11	9	9
	A–	A	A	A	A	A	A	a	A	A	A–	A–	A–
Facing dark	3	2	..	2	1	3	2	2	1	3	0	2	2
	A–	A–	..	S–	S	S	S	S	..	S–	..	S	S
In light end	5	7	6	7	6	8	8	9	6	4	7	9	8
	A–	A	A	a	A	A	A	a	a	a	A	A	a
In dark end	6	4	5	4	5	3	3	2	5	7	4	2	3
	A–	A	A–	A–	S–	S	A	S–	S–	S–	S–	S–	S

Observations	27	28	29	30	31	32	33	34	35	36	37	Totals
Facing light	8	8	8	7	8	9	8	7	5	5	4	298
	A	A	A	A–	S	S–	A–	A–	A	A	A–	
Facing dark	1	3	2	4	3	..	3	4	6	6	2	90
	S	S	S	S	S	..	S	S	S–	A–	A–	
In light end	9	7	9	7	4	4	4	4	5	3	4	244
	a	a	A	A–	A	A	A–	A	A–	A–	A	
In dark end	2	4	2	4	7	7	7	7	6	8	7	163
	S	S	S	S	S	S	S	S	S–	A	A	

For explanation of letters see page 32.

Observations 1 to 12 were made at night; the other observations during the morning and afternoon of the following day. Between observations 22 and 23 was an interval of two hours and five minutes during which the tungsten light was shining into the end of the aquarium. After observations 9 and 25 all the animals were gently pushed into the end of the aquarium away from the light. After observation 12 and about one hour before observation 13 the animals were fed as much raw meat as they would eat. It will be seen from table IV that the average activity of the animals facing the light was greater than that of the animals facing away from the light; and that the animals in the near half of the aquarium were, as a rule, more active than those in the half farther from the light. As before, animals which lay, at the moment of observation, with the long axis at right angles to the direction of the rays of light were not counted. The total number of animals facing the light was 298, to 90 that faced away from the light; the number in the near half of the aquarium was 244, to 163 in the half farther from the light.

Experiment VI.—Another series of 25 observations, taken every five minutes, under conditions similar to those just described, except that the aquarium was in an ordinary room and covered with the same black cloth, gave 200 facing the light to 78 facing away from the light, and 179 in the near end to 97 in the far end of the aquarium.

Experiment VII.—Still another series of 30 observations, taken every five minutes, was made upon nine of the same animals after having been in the dark for 32 days except for about two and one-half hours three days before the present experiment. This was to determine if prolonged residence in total darkness had any effect upon their reaction to white light. The arrangement of the apparatus was the same as in experiment V. One hundred and ninety-seven animals were found facing the light, to 72 facing away from the light; 202 were in the near half, to 74 in the far half of the aquarium.

It will be seen by comparison with experiment V that, after this long residence in darkness, the preponderance of animals that faced the light over those that faced in the opposite direction was less than in animals that had been in the light; while the preponderance of animals in the near half of the aquarium over those found in the distant half was greater in animals that had been in the dark than in those that had been in the light. It is possible that these differences may have been due to other causes than the prolonged residence in the dark.

Experiment VIII.—To see whether the same eleven animals were positively phototactic to a light of even greater intensity than the tungsten the aquarium, covered as before, with a black cloth, was placed, in a dark room, with its open end fifteen inches from the lens of an arc projection lantern. Observations were taken at five-minute intervals. At this distance the light was, of course, decidedly painful to the human eye.

The positive response was so marked that only 15 observations were made, which gave 116 facing towards the light to 41 facing away; and 105 animals in the near half of the aquarium to 60 in the distant half. The animals facing the light and in the near half were, as a rule, somewhat, though not a great deal, more active than the others.

It appears, therefore, that the response to white light is about the same whether the source of light be dim daylight or an intense electric arc.

Experiment IX.—This experiment was to determine the effect of low temperature upon the responses of Diemyctylus to white light at the end of the aquarium.

TABLE V

Observations ..	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Facing light. ..	..	..	..	1	0	0	7	2	2	3	5	2	3	0
				S			S–	S–	A–	A–	S–	S–	S–	
Facing dark. ..	..	..	..	10	11	11	4	9	9	8	6	9	8	8
				S–			S–	S–	A–	S–	S–	S–	S–	A–
In near end ...	..	..	..	1	0	0	7	6	5	6	7	4	3	0
	s	S	S	S			S–	S–	A–	S–	S–	S–	S–	
In far end.....	..	..	..	10	11	11	4	5	6	5	4	7	8	11
	s	S	S	S–	S–	S	S–	S	A–	S–	S–	S–	S–	A–

Observations ..	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Facing light. ..	0	2	4	4	6	2	4	3	4	3	3	2	5	4
					S	A–	A–	A–	A–	A–	A–	A–	A–	A–
Facing dark. ..	4	4	3	3	4	7	7	7	4	7	8	7	4	..
	A–				S	A–	A–	A–	A–	A–	A–	A–	A–	
In near end ...	0	0	0	0	10	7	7	4	4	2	2	2	2	2
					S	A–	A–	A–	A–	A–	A–	A–	A–	A–
In far end.....	11	11	11	11	1	4	4	7	7	9	9	9	9	9
	A–			S	S	A–	A–	A–	A–	A–	A–	A–	A–	A–

Observations......	29	30	31	32	33	34	35	36	37	38	39	40	Totals
Facing light......	4	4	3	5	7	2	4	4	6	3	3	6	122
	A–	A–		A–			A–	A–	A–	A–	A–	A	
Facing dark.	5	5	6	6	4	9	7	6	5	8	5	3	231
	A–	A–		A–			A–	A–	A–	A–	A–	A	
In near end.......	3	3	8	5	6	7	5	5	5	5	4	3	140
	A–	A–		A–			A–	A–	A–	A	A–	A	
In far end........	8	8	2	6	5	4	6	6	6	6	7	8	266
	A–	A–		A			A–	A–	A–	A–	A–	A	

The same animals and arrangement of apparatus were used as in experiment V, the only difference in the experiments being that in the present one, table V, the aquarium containing the animals had been placed outdoors for three hours, until the temperature of the water had fallen to 0° C. and a thin skim of ice had formed.

As in experiment II the animals at the beginning of the observations were all stationary, as though dead, and were evenly scattered over the bottom of the aquarium. Observations 1 to 6 were taken at ten-minute intervals; 7 to 40 were at five-minute intervals. After observations 5, 17 and 30 the ends were reversed, thus putting the animals from the far to the near end of the aquarium; this, of course, raised the total number for the far end and lowered the total number for the near end. For the first 3 observations, or one-half hour, practically no change in the position of the animals took place; at this point warm water was carefully added until the temperature of that in the aquarium was raised to 8.5° C., and by the end of the experiment the temperature had slowly raised until it was 12.5° C. After the addition of the warm water the animals began to show signs of life, though they remained rather sluggish to the end of the experiment.

In 40 observations 122 animals faced towards the light to 231 away from the light; 140 were in the near half of the aquarium, 266 in the half farther from the light.

Experiment X.—This was a continuation of the preceding experiment under exactly the same conditions except that the temperature of the water at the first observation was 4.5. C. instead of 0° C., and the animals were moving about very slowly instead of lying perfectly still. After the 4th, 5th and 14th observations all the animals were pushed into the near half of the aquarium. Observations were somewhat irregular, being every ten minutes for about the first half of the observation, every five minutes for the latter half of the observations. After observation 16 warm water was added until the aquarium temperature was 23.5° C.; the dark room being cold, this temperature was lowered 2° by the end of the experiment. In 28 observations 134 animals were found facing the light to 147 that faced away from the light; while 107 animals were counted in the near half of the aquarium to 212 in the far half. It is noticeable, however, that in the 16 observations before the warm water was added 67 animals faced the light to 83 that faced in the opposite direction, while in the 13 observations after the addition of the warm water 67 animals again faced the light but only 64 faced away from it. Again, in the first 16 observations 50 animals were counted in the near half of the aquarium to 126 in the far half, while in the last 13 observations 57 animals were in the near half to only 86 in the far half.

Experiment XI.—This was a continuation of experiment X on the following day. The water at starting was 5.5° C. and was raised, after observation 12 to 23° by the addition of warm water. The first 7 observations were at somewhat irregular intervals of ten minutes; the remaining observations were at five-minute intervals. In 30 observations 149 animals faced the light to 154 that faced in the opposite direction; while 143 were noted in the near end to 198 in the distant end. In the first 12 observations, however, when the maximum temperature of the water was 11°, only 43 animals faced the light to 73 that faced away from it; while in the last 18 observations, when the water had been raised to 23°, 106 animals faced the light to 62 that faced the other way. Again, in the first 12 observations 48 animals were in the near half to 94 in the far half, while in the last 18 observations the numbers were 95 to 104 respectively. In a total of 98 observations for the last three experiments, 405 animals faced the light to 532 that faced in the opposite direction; and 390 animals were counted in the near half of the aquarium to 676 that were found in the far half.

From the last three experiments it seems that low temperatures tend to inhibit or even reverse the positive phototaxis of Diemyctylus as seen in movements towards the light and orientation of the body so that the animal faces the light.

Experiment XII.—This experiment was to determine the responses of Diemyctylus to white lights of different intensities acting simultaneously at opposite ends of the aquarium.

Nine of the same animals used in the preceding experiments were employed here; they had been in darkness for 15 days. The same aquarium in the same dark room was used; it was entirely covered with black cloth except at the ends where the light entered. Two 25-watt, 155-volt tungsten lights were used; they were not tested as to candle-power, but they were of the same supposed power and were of the same age. One light was six inches from one end of the aquarium, the other light was twenty-four inches from the other end. The first 50 observations were taken at five-minute intervals, except that one and one-half hours intervened between observations 31 and 32, during which time the animals were in the darkness.

In 50 observations 265 animals were seen facing the more distant (24 inches) light to 170 that faced the nearer and, therefore, more powerful light. Two hundred and sixty-nine animals were found in the half of the aquarium nearer the more distant light, 174 in the region towards the nearer light. The weaker of these two lights, then, seems to have the greater attraction for the animals.

Experiment XIII.—The arrangements were exactly as in experiment XII except that the lights were six inches and twelve inches from their respective ends of the aquarium. Two and one-half hours in darkness intervened between observations 19 and 20. In 40 observations 141 animals were found facing the nearer (6 inches) light to 185 that faced the more distant light; while 163 were found in the half of the aquarium towards the nearer light, to 190 in the other half. The weaker of the two lights seems again to be the more attractive to the animals, though in a less marked degree than in experiment XII.

Experiment XIV.—The same experimental conditions as in the preceding except that the lights were twelve inches and forty-eight inches from their respective ends. Between observations 15 and 16 was an interval of three days, and between observations 45 and 46 was an interval of one day; during both intervals the animals were in the dark. As in the preceding experiment, the observations were taken every five minutes.

In 60 observations 289 animals were found facing the nearer (12 inches) light, to 229 that faced the farther (48 inches) light. Two hundred and eighty-three were seen in the half of the aquarium towards the nearer light, to 255 in the other half. It seems that, while the differences between these sets of figures are not great, the nearer (12 inches) light has a somewhat greater attraction than the more distant (48 inches) light.

Experiment XV.—The conditions of this experiment were exactly the same as in the preceding except that the lights were twenty-four inches and seventy-two inches from their respective ends. There was an interval of twenty-one hours (in the dark) between observations 5 and 6. In 40 observations 203 animals faced the nearer (24 inches) light, to 133 that faced the farther (72 inches) light; and 204 were in the half of the aquarium towards the nearer light, to 144 in the other half.

Experiments XII to XV may thus be placed in tabular form for comparison:

Experiment XII	6″ distance	facing 170
		near 174
	24″ distance	facing 265
		near 269
Experiment XIII	6″ distance	facing 141
		near 163
	12″ distance	facing 185
		near 190
Experiment XIV	12″ distance	facing 289
		near 283
	48″ distance	facing 229
		near 255
Experiment XV	24″ distance	facing 203
		near 204
	72″ distance	facing 133
		near 144

Experiments XII and XIII seem to indicate that when one of two sources of light is very intense the animals tend towards the less intense light; while experiments XIV and XV show that when neither source is very intense, perhaps not reaching a certain optimum, the animals tend towards the more intense light.

REACTIONS TO RED LIGHT

Experiment XVI.—In this experiment the same nine animals and the same arrangement of apparatus as in experiment V were employed; but between the tungsten lamp, placed six inches from the end of the aquarium, and the aquarium was a filter composed of two glass jars each 20 mm. thick containing an aqueous solution of crystal violet and of potassium monochromate respectively, after the formula of Landholt.

In 30 observations, taken at five-minute intervals, 225 animals were noted facing the red light to 46 facing away from the light; and 221 animals were found in the end of the aquarium nearer the light to 49 in the farther end.

Experiment XVII.—This experiment was an exact repetition of experiment XVI, made thirty days later, during which period the animals had been in the darkness of the photographic dark room. In 12 observations, at five-minute intervals, 86 animals faced the red light to 19 that faced in the opposite direction; and 82 were seen in the red end of the aquarium to 26 in the other end. Comparison of experiments XVI and XVII with experiment V shows that the proportion of animals attracted by the light was greater with the red light than with the white. This may have been due to the decrease in intensity rather than to the red color.

REACTIONS TO BLUE LIGHT

Experiment XVIII.—This experiment was performed thirty-six hours after experiment XVII; during the interval the animals were in complete darkness. The experiment differed from the other only in the substitution of a blue filter for the red. This filter consisted of two similar glass jars containing solutions of crystal violet and copper sulphate after Landholt's formulae. The five-minute intervals between observations were somewhat lengthened on four occasions by interruptions to the experiment.

In 30 observations 197 animals were found facing the blue light to 73 that faced away from it; 195 animals were found in the half of the aquarium near the light to 84 in the other half. It is evident that the proportion of animals attracted by the blue light is less than was attracted by the red light.

REACTIONS TO GREEN LIGHT

Experiment XIX.—The arrangement of this experiment differed from the last only in the substitution of a green filter for the blue. This filter consisted of solutions of copper chloride and potassium monochromate, after the formulae of Landholt, in jars like those described in the two preceding experiments. The same nine animals were used; they had been in total darkness for twenty-nine days, and had been fed upon earthworms the day before the experiment. In 30 observations, at five-minute intervals, 210 animals faced the green light to 51 that faced away from it; and 199 animals were found in the near half of the aquarium to 71 in the half farther from the light.

The attraction of the green light is apparently more marked than the blue but less marked than the red.

REACTIONS TO WHITE LIGHT ON VARIOUS PARTS OF THE BODY

Experiment XX.—In order to be able to throw a small, sharply-defined spot of white light on any part of an animal a small electric bulb was mounted in the tube of a microscope, as described by Bradley M. Patten in *Science*, January 22, 1915, pp. 141-2. By using different low-power objectives a sharply defined spot from 1 to 5 mm. in diameter was directed upon all parts of the body of several animals. These animals were in a black rubber developing tray in sufficient water to cover them. In one case they had been in a dark room only an hour; in another series of trials they had been in the dark for a week or more. Some of the animals were of the lighter shade with very bright crimson spots; other animals were of the darker type when experimented upon. During experimentation just enough light was admitted to the dark room to faintly see the animals, so that any movement could be noted. The spot of light was thrown, as has been said, on all parts of the body, from the head to the tip of the tail; on the crimson spots and between them; it was varied in diameter from 1 to 5 mm. No certain reactions could be determined for any of the animals used. Doubtful reactions were sometimes obtained when the spot was made large enough to cover the entire anterior half of the head.

When the spot was thrown on the black bottom of the tray near the animals they followed it actively and snapped at it, evidently taking it for food; they seemed to be able to see the spot at a maximum distance of about 3 cm.

Experiment XXI.—The same animals that failed to respond to the white spot from the microprojection apparatus responded promptly when a beam of sunlight was thrown, by a small mirror, upon various parts of the body. When the light was thrown upon the tail they either started forwards suddenly or drew the tail sharply forward along the side of the body. When the light was thrown upon the head the animal usually backed away from it. Animals in a cloth covered aquarium in a brightly lighted room responded about as promptly as those in the dark room.

Animals that had been for some time in the dark responded more promptly than those that had been exposed to the light; some of the former fairly jumped when the beam fell upon them.

Little or no response was obtained when a small beam from a 5 mm. mirror was used instead of a beam that was large enough to illuminate a large area of the animal at one time.

The animals responded in the same way, and almost as promptly, to a beam of light from below.

These reactions to a beam of sunlight are quite similar to those described by the author for Necturus (2).

SUMMARY

1. Under the conditions of these experiments Diemyctylus is almost always markedly negative in its phototropic reactions to white light, at ordinary temperatures.

2. At temperatures near 0° C. and 36° C. Diemyctylus is indifferent to white light from above.

3. The above reactions are the same whether the light fall from above or come from below, though they are usually less marked in the latter case.

4. Diemyctylus is positively phototactic to lights of all intensities, from very weak daylight to an intense arc light.

5. At low temperatures this phototactic reaction is inhibited or reversed.

6. With an intense white light at each end of the aquarium the animals tend towards the less intense light; if neither light be of great intensity, perhaps not reaching a certain optimum, the animals tend towards the more intense light.

7. Phototactic reaction to pure red light was the same as to white light, possible a little more marked.

8. The reaction to green light is the same as to the red, but less marked.

9. The reaction to blue light is the same, but still less marked.

10. A small spot of white light from a micro-electric torch produced no effect when thrown upon various parts of the animal's body.

11. The animals responded promptly to a beam of sunlight thrown on various parts of the body, either from above or below, by a small mirror, though if the mirror threw a beam of 5 sq. mm. or less there was little or no response.

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2. Reese, A. M. Observations on the Reactions of Cryptobranchus and Necturus to Light and Heat. *Biol. Bull.*, **11**, pp. 93-99. 1906.
3. Sayle, Mary Honora. The Reactions of Necturus to Stimuli Received Through the Skin. *Jour. Animal Behav.*, **6**, pp. 81-102. 1916.

ADDENDUM

As a check upon the preceding laboratory experiments, the following experiments were tried upon a number of newts of the same species, under as near natural conditions as could be obtained. The work was done, during the latter part of August, in a small, fresh-water pond, about two miles from the laboratory at Woods Hole, Mass.

Twenty-eight animals were obtained by sweeping a dip net through the grass of this shallow pond. They were caught during the morning, and were confined until night, and during intervals between experiments, in a 12 in. x 12 in. floating live-box, with wire top and bottom, which was partly filled with grass and dirt from the pond.

During experimentation they were confined in a cage 1 ft. x 2 ft. in area, 6 inches deep, and open above, made of one-quarter inch wire netting. This cage was sunk about 5 inches into the water so that it was surrounded by the grass of the pond. A few of the animals escaped, during the experiments, by climbing out of the cage.

Only sunlight and artificial white light were used, the latter being supplied by a miner's acetylene lamp with a reflector; this lamp gave a fairly brilliant though rather variable light, but its candle-power was not determined.

Experiment XXII.—This experiment was performed during a fairly dark, moonless night. One-half of the wire cage was covered with a board, while the other half was brilliantly illuminated by the acetylene lamp, fixed about 10 inches above the surface of the water. Fifteen observations, at 5-minute intervals, were taken, during which 65 animals were noted in the light half of the cage to 355 in the darkened half of the cage,—a proportion of more than five to one. This proportion would have been still greater but for the fact that after observations 2, 6 and 11 the light and dark ends were suddenly reversed, thus throwing the larger group of animals into the light area.

Experiment XXIII.—In this experiment the same cage and animals were used, but the light was bright sunlight. Of course, on account of the diffused light, the shaded half of the cage was not nearly so dark as in the preceding experiment. In 16 observations, at 5-minute intervals, 103 animals were counted in the light half of the cage to 297 in the dark; this proportion of nearly three to one would have been greater but for the sudden reversal of light and dark ends after observations 9 and 12.

It is evident, then, from experiments XXII and XXIII, that under these conditions the negative phototropism to white light is even more marked than in the laboratory experiments.

Experiment XXIV.—In this experiment the acetylene light was placed in a large, glass aquarium jar, which was sunk into the water of the pond so that the light was thrown into one end of the wire cage, the observations being made, of course, at night. This arrangement was not very satisfactory, as the dark color of the pond-water made the illumination of the far end of the cage very dim.

In 26 observations, at 5-minute intervals, 213 animals were noted in the half of the cage nearer the light to 263 in the farther half. After observations 9, 20, and 22, since it was difficult to reverse the ends of the cage, all the animals were pushed into the light half; this tended to decrease the excess of those in the dark end; but the experiment was hardly conclusive, perhaps on account of the unsatisfactory conditions.

Experiment XXV.—This experiment was performed with the clear sun shining down upon the end of the submerged cage, at an angle varying from 40 to 25 with the surface of the pond.

The cage being uncovered, the light was evenly distributed over the bottom, but entered, as said, from one end. Under these conditions, in 16 observations, at 5-minute intervals, 191 animals were noted in the half of the cage towards the sun, to 120 animals in the other half. After observations 8, 11, and 14 all the animals were gently pushed to the center of the cage, which diminished the preponderance of those in the half towards the sun. This experiment seems to indicate that, where the light is sufficiently bright, the animals tend to go towards it, as in the laboratory experiments.

These outdoor experiments, then, seem to substantiate, so far as they go, the results of the laboratory experiments.

THE INTERFERENCE OF AUDITORY HABITS IN THE WHITE RAT

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I

The present paper has grown out of the work which one of the authors has already published on audition in the rat.[1] On pages 324-5 of the last of these a report is made of some tests on the retention of auditory habits. It was these tests that gave us our cue. Negative results only had been secured by attempting to train rats to turn in one direction through a box when a tone or a chord was sounded and to turn in the opposite direction when silence was given. This was a direct attack upon the problem of tone sensitivity by the association method. It occurred to us that working indirectly through habit interference further data of value might be secured. By such a method one could redetermine whether for the rat certain tones are equivalent to silence. Should such a method succeed, its data would be similar to that secured by the conditioned reflex method. In the present paper we shall deal only with the tests bearing upon habit interference. An immediately succeeding article will stress the auditory sensitivity data secured by this method and combine them with other observations from this laboratory.

The same T-shaped discrimination box was used here that has been described in the previous papers. The buzzer was held on a wire over the apparatus in the same location indicated for the tuning forks. The initial plan (which was much supplemented as will be seen) called for 20 rats as follows:

A. 20 rats train to turn rt. for handclaps, lft. for silence.
B. 4 rats of set A train for 30 days to turn rt. for buzzer.

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[1] Hunter, Walter S. The auditory sensitivity of the white rat. *Journal Animal Behavior*, vol. 4, p. 215, 1914, and vol. 5, p. 312, 1915.

C. 4 rats of set A train for 30 days to turn rt. for tuning fork 256 d. v.
D. 4 rats of set A train for 30 days to turn lft. for tuning fork 256 d. v.
E. 4 rats of set A train for 30 days on regular series of presentations on auditory stimulus.
F. 4 rats of set A tested for retention after 30 days rest.
G. Rats of sets B, C, D, E retested on handicaps.

This program calls for a measure of the relative retention of a simple co-ordination in five groups of animals, each group having been kept under different conditions for an interval of thirty days.

Only 18 rats completed the work of set A. Of these 13 were females (numbers 1, 4, 9, 10, 11, 14, 15, 16, 18, 19, 20, 21, 24), and 5 were females (numbers 7, 8, 17, 22, 23). All were about three months old at the beginning of the tests. With the exception of nos. 1 and 4, they were untrained. No. 1 had been trained on the inclined plane problem box. No. 4 had worked with light in a two-choice discrimination box. Nos. a, b, c, 25, 26, 27, 28, 29, whose records are given below, were also about three months old at the beginning of the tests. All of these animals were females. The tests here reported, like most studies of animal learning, have been long and tedious. They have extended from January, 1915, to June, 1916.

Prior to the regular tests, each rat was fed on the experiment table and was permitted to run through the box on each of two days. Care was taken that no position habits were developed. Those rats that manifested a preference for a certain side of the box were immediately forced through the opposite side.

Discrimination was regarded as established when the average percentage of correct reactions for four days together was 87½% with no one day's record below 80%.

II

Learning the first habit.—Table 1 gives the total number of trials required by each rat to set up the habit of running to the right for handclaps and to the left for silence. The period of learning is the period up to the 40 trials made at the standard per cent. The rats underscored are males. Figure 1 shows the distribution curve. All but six of the rats had mastered the problem within 500 trials. I am inclined to attribute the irregularities largely to position habits which appeared during the learning and which had to be overcome. Fear caused by punishment retarded the last part of the learning in rats 25-29. No sex differences appear. The form of the learning curve will be shown in section VIII.

TABLE 1

NUMBER OF TRIALS PER RAT IN LEARNING FIRST HABIT

Rat	Trials	Rat	Trials	Rat	Trials
1	260	16	260	a	350
4	210	17	300	b	420
7	430	$\overline{18}$	450	c	460
$\overline{8}$	500	19	450	25	420
$\overline{9}$	300	20	710	26	550
10	390	21	610	27	320
11	370	22	620	28	610
14	370	$\overline{23}$	470	29	570
15	360	$\overline{24}$	260		

Each rat of set A, when it had completed its four days with a general average of 87½%, was given three controls, each of which in general alternated with a day on the normal stimulus of handclaps. Control 1—no stimulus was given. The reaction was counted correct if it agreed with the series of presentations. This control was to test the animal's dependence upon extra-auditory cues. Control 2—an electric buzzer was sounded in place of the handclaps. This control was given to each rat on each of four successive days (40 trials). Control 3—a tuning fork, 256 d. v., placed over the apparatus as described in previous papers, was sounded by striking with a felt hammer. This tone was substituted by the experimenter for the handclaps. The necessity for the first control needs no comment. Controls 2 and 3 were used in order to determine the relation of the respective stimuli to the habit just established. It is very important, if interference effects are to be studied, that the mutual relations of the stimuli (i.e., their transfer relations) be known,—in the present case, whether the buzzer and the tuning fork would be substituted readily for the handclapping in this particular co-ordination.

The results of control 1 indicate that the animals were depending upon auditory cues. Only one rat's (No. 17) record was

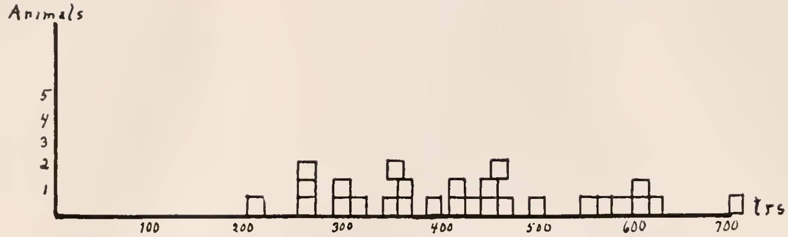

FIGURE 1.—Distribution curve of the original learning

the least ambiguous. The accompanying table (No. 2), however, will show that an extended use of the control produced low percentages. Control 2, where the buzzer was substituted, gave the following results: On the first day, 7 rats (Nos. 15, 18, 20, 22, 9, 10, 11) made below 80%. On the second day, 5 rats (Nos. 20, 22, 10, 11, 14) made below 80%. On the third day, 3 rats (Nos. 21, 8, 11) made below 80%. On the fourth day, Nos. 9 and 14 fell below 80%. Seven rats (Nos. 1, 4, 7, 16, 17, 19, 23) never fell below 80%. The adjustment or transfer was thus usually made either at once or by the end of the second day. On control 3, 6 rats at different times made a day's record with 80% correct. This occurred, however, with a majority of days at 50, 60 and 70% and is to be regarded not as evidence of auditory sensitivity, but as an accident in the grouping of kinaesthetic factors.

TABLE 2

RECORDS ON CONTROLS GIVING CORRECT CHOICES OUT OF 10
The text states that not all records are from successive days

Rat	Con. 1	Con. 2	Con. 3
15	6, 5, 6	5, 10, 8, 8	7, 6, 7
16	7, 4, 5	8, 9, 10, 8	6, 6, 8, 6
17	8, 5, 7, 8, 6, 5	8, 9, 8, 9	8, 7, 7, 10, 7, 7
18	5, 6, 6	6, 8, 9, 10	8, 9, 5, 8, 5
19	4, 5, 7	10, 10, 9, 9	6, 7, 8, 7
20	6, 6, 6	7, 5, 10, 9	6, 6, 5
21	6, 6, 5	9, 9, 6, 9	7, 6, 7
22	6, 5, 5	7, 6, 8, 10	6, 7, 4
23	5, 5, 7	8, 8, 9, 9	7, 8, 7, 7
1	6, 5, 6	10, 8	6, 5, 5
4	6, 7, 5	9, 10, 8, 9	6, 7, 5
7	7, 7, 6	9, 10, 8, 8	5, 7, 7
8	5, 6, 6	9, 8, 7, 8	6, 6, 7
9	6, 6, 6	6, 8, 9, 6	5, 6, 5
10	6, 3, 4	7, 5, 8, 10	7, 6, 6
11	5, 3, 5	7, 5, 6, 9	7, 6, 8, 6
14	6, 5, 6	8, 7, 9, 6	5, 6, 7

Table 2 presents the results for these controls. The four days' records preceding control 1 were made at or above 87½% correct. Each day's record with controls 1 and 3 alternated with a day on the normal stimulus (handclaps) save when 80% was made. In these cases the same control was used on the succeeding day.

III

Thirty-day Tests.—After control 3 had been given, each rat of set A received the normal stimulus for four days or until the standard 87½% was reached. The animals were now started upon the interference periods (B-E) as outlined above for 300 trials or 30 days. No rat learned his problem within this period. Only one rat (No. 15) made 80% during any one-sixth (50 trials) of the period. This rat made 82% during the third 50 and 84% during the fourth 50 trials. (These are general averages for the 50 trials.) After this he broke down, so that on the final sixth 50% only was made. There is no available explanation for this. Neither fear nor position habits intervened. It is one of those anomalous cases that will occur. (It took this rat 180 trials to relearn the normal habit. This, however, cannot be correlated with the high percentage in the interference period because long periods of relearning appeared in other rats where the high percentages were absent.) Each of the succeeding 50 trials for the rats in these sets averaged practically between 50 and 65%. Table 3 contains a record of the number of correct reactions in each 50 trials made by each rat during the 30 days.

TABLE 3

TRIALS CORRECT IN EACH 50 DURING THE 30-DAY TEST AND THE RELEARNING

30-day training

Sets	B			C				D				E			F			
Rats	15	23	7	11	1	17	18	16	14	10	20	9	19	21	4	24	8	22
	28	31	13	20	28	32	29	35	29	27	26	24	28	14	..	..	..	..
	32	34	19	25	26	27	27	43	33	26	32	24	28	15	..	..	..	..
	41	29	23	24	23	26	24	34	33	35	24	27	30	19	..	..	..	..
	42	33	26	30	20	31	26	33	35	27	26	25	33	21	..	..	..	..
	31	17	24	19	27	21	28	35	26	32	29	30	28	21	..	..	..	..
	25	28	27	20	23	29	24	33	28	28	29	29	27	19	..	..	..	..

Relearning

36	35	24	46	37	38	35	38	39	44	35	34	37	45	37	45	33	29
33	of	36	..	42	37	10	..	of	10	of	of	of	9	of	..	37	39
41	40	of	..	41	35	of	..	40	of	40	40	40	of	40	..	40	27
39	..	40	..	9	37	10	..	..	10	..	..	..	10	..	..	42	of
9	..	..	..	of	40	..	..	..	..	..	..	..	..	..	..	41	30
of	..	..	..	10	18	..	..	..	..	..	..	..	..	..	..	16	..
10	..	..	..	..	of	..	..	..	..	..	..	..	..	..	..	of	..
..	..	..	..	..	20	..	..	..	..	..	..	..	..	..	..	20	..

Total trials on relearning

210	40	90	50	160	270	60	50	40	60	40	40	40	60	40	50	270	130

On the day following the close of the 30-day period each rat was retested on handclaps to the right. The results are included in table 3. Our criterion of the degree of retention has been the length of the period of relearning rather than the per cent of correct reactions on the first day. Table 4 shows that in the present case there is no way of predicting the amount of relearning from the percentages made on the first days. It will be seen from table 3 that all sets of rats are essentially on a par with respect to retention. In other words, so far as these rats are concerned, 30 *days of diverse training has not produced effects in retention.*

TABLE 4

F stands for number of trials correct in first 10 of relearning.
T is the total relearning time in trials.

B			C			D			E			F		
Rat	F	T	Rat	F	T	Rat	F	T	Rat	F	T	Rat	F	T
7	5	90	1	5	60	10	8	40	9	7	40	4	9	40
15	3	210	11	10	50	14	10	40	19	9	40	8	7	270
23	8	40	17	7	270	16	8	50	21	9	60	22	2	130
			18	2	160	20	8	40				24	7	50

IV

Sixty-day Rats.—Four rats (Nos. 1, 11, 17, 18) had been tested in the work outlined above. During the 30-day period an effort was made to train them to turn right for the tuning fork 256 d. v. without success. These rats were then idle, although kept in good physical condition, for the following intervals of time: Nos. 1 and 11 went 10 days; No. 17 went 23 days; and No. 18 went 40 days. At the close of these intervals of time, all of the rats were brought back to the standard percentage of correct reactions on turning to the right for handclaps. They were then put into training again on going right for 256 d. v. and left for silence. They remained in this series for 600 trials, 10 per day, punishment and reward. No. 11 was the only rat of the four that improved during the 60 days. He learned the reaction in 270 trials. The senior author was away for the summer at this time and no control tests were made to determine the basis of the response. Inasmuch, however, as no other rat in the laboratory has learned to react to tone in this fashion since the work was begun in 1913, and inasmuch as this rat learned rapidly, it is most probable that the reaction was due to secondary cues accompanying the tone. This experiment is confirmatory of work previously published indicating the insensitivity of the rat to certain tones.

At the close of the 600 trials, retention tests for handclaps to the right were given. No. 1 came back to standard in 10 trials; No. 17, in 60; and No. 18, in 30. This is practically perfect retention and is as good a record as that made by the 30-day rats. The results are practically comparable, although not absolutely so inasmuch as the 60-day animals were somewhat overtrained relatively on h. c. to the right.

The same results with the same limitations were secured with rats 4, 8, 22 and 24. These were the rats listed under F in the 30-day tests. The retention tests in that series brought these animals back to the standard. They were then idle for 60 days at the close of which period they were again retested on h. c. to the right. Rat No. 4 came back to standard in 20 trials; No. 8, immediately; No. 22, in 30 trials; and No. 24, in 40. In order to compare the results given here and in the above paragraph with those listed under "Total trials on relearning" in table 3, it is necessary to subtract 40 from each of the totals in that table. The results given in the present section are the number of trials up to the 40 made at the standard per cent.

Rats Nos. 7, 15 and 23 had been through the 30-day tests in set B,—turn left for the buzzer. After intervals of rest as follows they were brought back to standard on handclaps: No. 7, 9 days; No. 15, 38 days; and No. 23, 47 days. They were now retrained on going to the left for the buzzer and to the right for silence. The intention was to train them upon this for 60 days, unless the habit was established sooner, and then test their retention of h. c. to the right. Rat No. 7 learned in 54 days, 540 trials; No. 23 learned in 35 days, 350 trials; and No. 15 learned in 45 days, 450 trials. If we add to this only the 300 trials which they had previously had on the same problem in the 30-day test, No. 7 learned in 840 trials; No. 15, in 750 trials; and No. 23, in 650 trials.

At the close of the 40 trials at the standard percentage for rats 7, 15 and 23 as just noted, they were retested on h. c. to the right. No one of the three fell below 80% for 30 trials. In other words, there was perfect retention. When given control 1—tests made without the auditory stimulus—the percentages ranged between 30 and 50. On one day and with only one rat did it go as high as 70%. So there could be no doubt that the rats were dependent upon the auditory stimulus. Here we have a case where two opposite habits are present simultaneously in the organism although the respective stimuli were not originally differentiated. The process of the differentiation has been a successive formation of habits and not a simultaneous one as is usual in discrimination tests. And the interesting thing is *that the formation of the second (and opposite) habit has not interfered with the retention of the first habit. A second automatism has arisen gradually and independently of the first.*

Further tests were made upon rat No. 7 to determine the nature of the difference between the buzzer and the handclaps. These results will be published in a separate paper.

V

Ninety-day Rats.—Three untrained rats, Nos. a, b and c, were trained to go right for handclaps and left for silence. The number of trials required in learning is shown in table 1. At the close of this series, control 1 was alternated with normal for three days in order to be sure that the animals were not depending upon extra-auditory cues. The percentages were all around 50. These three rats were then given a period of idleness for 90 days. During this period, they remained in splendid physical condition for experimentation. At the close of the period, they were retested on h. c. to the right. It is needless to give the data in detail. No one of these rats averaged above 70% for any 50 trials although their retraining extended through from 34 to 45 days. Their behavior at the beginning of the retesting indicated that the apparatus and method were still familiar to them, but that was all. The results as a whole indicate that these rats had lost all measurable traces of the original training. It may be well that in a habit so difficult as the present one continued or retained familiarity is too slight an aid to manifest itself in shortening the period of relearning. The disintegration of this habit in the white rat apparently takes place between 60 and 90 days. The 60-day tests indicated practically perfect retention at the close of that period, but the two sets of data are not strictly comparable. The rats in the 60-day tests had been retrained at different intervals on h. c. to the right after the original learning. Hence the habit was considerably overlearned.

VI

Effect on retention of learned vs. unlearned habits.—It would be interesting to know just what went on in the rats' nervous systems during the 30 and 60-day periods of training. We seem forced to assume that certain synaptic connections have persisted in spite of the attempts of incoming stimuli to disintegrate them. Inasmuch as either continued training (?) or the lapse of time will result in the disintegration of these connections, definite problems arise under each condition. We have indicated that with the mere lapse of time, the dissolution of the particular habit in our rats occurred between 60 and 90 days. The present section contributes data throwing light upon the comparative disintegrations brought about in the h. c. habit by the 30 days' ineffective training on B and by a period of training during which B was mastered.

Of the 18 rats used on the 30-day test described above, 9 made the standard 87½% immediately upon being re-tested on h. c. to the right. Four others did essentially as well. Two hundred and seventy trials was the maximum period of relearning and was found in two rats. Table 3 gave the data in detail. It will also be recalled that no one of these rats improved during his 30-days' training upon B.

Three untrained rats, Nos. 26, 27 and 29, formed the original h. c. habit as indicated in table 1. They were then trained on B until it was mastered. (I shall discuss certain details of this training in a following section.) At the close of the 4 days on B made at 87½%, these rats were retested on h. c. The results for all save the original learning are given in table 5.

TABLE 5

Correct in successive 50 trials in learning B

No. 25	No. 26	No. 27	No. 29
14	15	15	5
10	15	19	20
18	20	22	18
17	12	38	21
18	22	36	21
19	21	33	19
20	22	30	17
22	20	34	24
25	29	33	32
28	32	38	36
28	37	34	29
30	37	36	31
29	34	32	34
31	38	38	35
34	39	38	36
34	37	15 of 20	39
42	38		32
Unfinished	32		41
	7 of 10		13 of 20

Correct in each 50 in retest on h. c.

	29	36	26
	31	36	35
	30	32	24
	31	33	33
	36	38	34
	24 of 30	41	8 of 10
		8 of 10	

No 26 required 280 trials for the re-learning here in question. No. 27 required 310; and No. 29, 260 trials. The intervals for 26 and 29 are a little too small inasmuch as these two rats grew sick and died. Each, however, had reached 80% correct and so was within 7½% of the standard. The indications from this test are that marked progress must be made in the formation of a second contradictory habit before the retention of a first habit is noticeably affected. This can be represented graphically as indicated in figure 2. The three lines to the left are based upon rats 26, 27 and 29. The three lines to the right are based upon the 18 rats of the 30-day test. The first line in each column represents the average number of trials in learning the original h. c. habit; the second line, the trials given on habit B; and the third line, the re-learning time. The detailed data have already been given in the tables. The rats represented in the right hand column averaged about 5 months old at the beginning of the relearning tests. This was approximately 2 months younger than the other set of animals at the corresponding point of their tests. Both sets were composed of active animals, however, and in view of the marked difference in results as compared with Hubbert's,[2] I am inclined to discount age as an important factor in determining the present data.

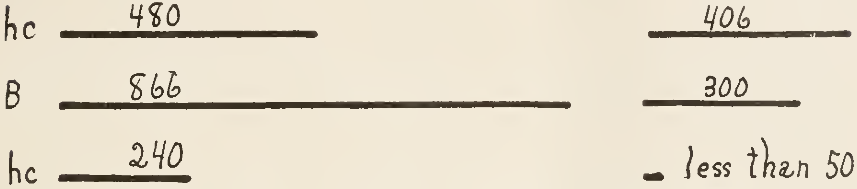

FIGURE 2.—Effects on retention of learned *vs.* unlearned habits.

A comparison between these data and the results of the 90-day test points the way toward interesting interpretations. The 90-day rats had lost all measurable traces of the original h. c. habit whereas rats 26, 27 and 29 relearned within an average of 260 trials or 26 days. These three rats had spent 85 days on habit B. Unless these are accidental variations, then, it would seem that the training on B favored the retention of h. c. The rats seemed equal in physical fitness for the tests. If we now consider the relations of the data given in figure 1, it would seem that *the loss in retention of the first habit is probably caused as much or more by the lapse of time than by the formation of the contradictory habit.* It was found in the 30-day test that training had no greater effect on retention than lack of training. *It is thus suggested,* although not clearly proved by our tests, *that the disintegration of certain habits in the rat is due to a temporal factor and not to habit interference.*

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[2] Hubbert, H. B. The effect of age on habit formation in the albino rat. *Behavior Monographs,* 2, no. 6, 1915.

VII

The Strength of Habit.—Rats 25, 26, 27, 28 and 29, whose learning periods were described in the first section of the paper, were further tested as follows: At the close of the 40 trials at 87½% made on the first h. c. habit, each rat was given control 1 on three days alternating with the normal. All of the rats failed to respond correctly in this control. They were then each given two consecutive days on control 2 (buzzer substituted for h. c.). In case a rat fell below 80%, a day with the normal stimulus was interpolated. The results are in table 6.

TABLE 6

	No. 25	No. 26	No. 27	No. 28	No. 29
H. C.	9	10	9	8	8
Con. 2	8	6	9	8	3
H. C.	..	8	..	..	8
Con. 2	9	7	8	..	8
Con. 2	..	..	8	..	..
H. C.	..	7	..	..	8
		8			

It will be seen from this that rat 26 did not rate the buzzer as identical with the handclaps and that No. 29 failed also, but on the first day only. No 28 became sick on the third day and was dropped from the tests. At the close of the tests in the above table, Nos. 25, 26, 27 and 29 were immediately started on learning " buzzer to left, right for silence " which was the opposite habit to the extent shown in the table. The progress of learning B in successive fifties was shown in table 5. The very important point that I wish to emphasize is that no one of these four rats learned in less than 770 trials while two were as high as 910 and 920. *It took these rats approximately twice as long to break the h. c. habit as it had to form it.* The figures are: No. 25, h. c. habit-420, buzzer habit-850 (?); No. 26, h. c. habit-550, buzzer habit-910; No. 27, h. c. habit-320, buzzer habit-770; No. 29, h. c. habit-570, buzzer habit-920. These figures exhibit in a striking manner the tenacity of habits in the rat. The original habit need not be literally broken, however, because in each case a period of retraining reinstated it. The situation is probably more accurately described by saying that the first h. c. habit interfered with the formation of the buzzer habit, although the latter but slightly (if at all) affected the former. The amount of the interference will probably depend much upon the ease of discrimination between the stimuli for the two habits. We are not prepared to contribute upon this point. (Because the rats ranked the buzzer as the same as handclaps we have felt justified in assuming that untrained rats would learn " buzzer to the left " as readily as " hand claps to the right.")

Mrs. Binnie Pearce, in research from this laboratory as yet unpublished, found even more striking interference in visual habits. Using the same T-shaped box, she trained rats to run one way for light and the other way for darkness. When she then attempted to train them to reverse this behavior, the task was found all but impossible.

We are not familiar with any other work where an animal has had to learn the opposite of a previously acquired habit. There are many cases where different habits have been set up in succession and where interference has been more or less explicit. However, in order to secure comparable data, it is necessary that the stimuli be known and the responses simple. The study of interference in mazes, latch boxes, etc., suffers for this reason. Not only must the stimulus be known in the case of the first habit, but the second stimulus must be known physically and also physiologically in terms of the first one. Thus one can know whether or not the stimulus for the second habit is for the subject in that situation the same as the first stimulus (positive transfer). Where the type of habit set up is kinaesthetic as opposed to auditory or visual, the control of the stimulus is very difficult because the stimulus lies in the animal's movements. The most feasible procedure is to reduce the problem to such an extent that only one or two prominent kinaesthetic experiences are presented. The senior author is working upon this problem at the present time, although interference is but one phase of the study.

VIII

Relative rates of error elimination in interfering habits.—With particular reference to the 30-day rats and rats 25-29, it is of interest to raise the following question: In what parts of the learning curves does the interference, as measured by the relative rates of error elimination, occur?

Table 7 gives data for rats 25, 26, 27 and 29. The numbers represent the percentages correct in each succeeding one-tenth of the learning process.[3] The first columns for each rat are the records for learning the original h. c. habit. The second columns are the records for learning B. These figures are secured as follows: No. 25, e.g., learned h. c. in 420 trials. This is divided into 10 parts of 42 each. Of the first 42, 21 or 50% were correct. This method when applied to all members of the group enables us to construct a curve which throughout its length is representative of the group. The bottom numbers in each column of table 7 represent the percentages of correct reactions made in the last 40 trials. Sometimes this runs over the standard 87.5%. The values above S are from the forties made at or above the standard per cent.

TABLE 7

25		26		27		29		Av.	
50	23	54	29	50	31	50	23	51	26
57	34	63	29	50	45	70	39	60	36
57	37	38	35	43	75	64	42	50	47
57	38	60	45	59	64	68	35	50	45
78	50	54	49	43	64	61	58	59	55
66	53	72	67	59	70	64	64	65	63
64	60	61	71	75	68	70	64	67	65
59	59	76	73	65	71	77	69	69	68
59	68	76	75	75	71	82	82	73	74
78	76	74	71	81	75	66	75	74	74
87.5	90	87.5	87.5	90	87.5	90	90	88	88

If the curves of figure 3 are examined, the curve for B is seen to start much lower than the curve for h. c. and to lag markedly behind throughout eight-tenths of the learning. (These curves are plotted from the average values in table 7.) This lag would be even greater, but for the accidental fact that learning h. c. was retarded toward the last by the fear that arose in the rats from punishment. The marked interference of the two habits is seen when the last of h. c. is compared with the first of B, and also when the first parts of the curves are compared. B is more than a new habit. It is interfered with from the start by h. c.

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[3] This method of treating the learning process is taken from Dr. S. B. Vincent's Function of the vibrissae in the behavior of the white rat. *Behavior Monographs*, **1**, no. 5, p. 17, 1912.

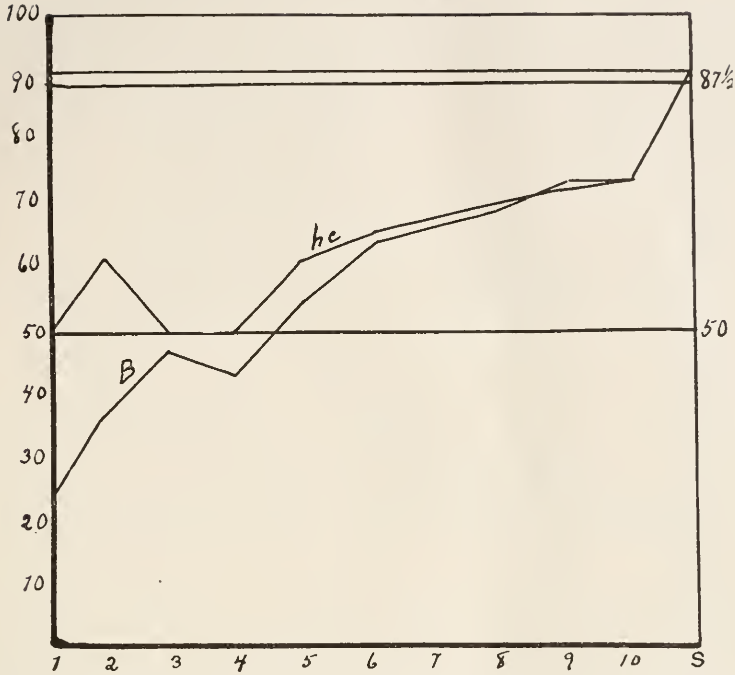

FIGURE 3.—The relative rates of error elimination in the hand clapping habit and the buzzer habit. Based on rats 25, 26, 27 and 29.

TABLE 8

15		23		7		Av.	
52	57	57	48	39	46	49	50
52	57	61	65	48	50	53	55
61	64	61	60	51	48	57	57
36	55	70	65	55	53	53	57
63	68	59	54	62	48	61	56
63	75	59	54	69	57	63	62
80	55	76	57	83	51	79	52
88	71	76	68	67	55	77	64
83	75	72	65	86	59	80	66
66	71	78	51	67	61	70	61
95	90	90	90	87.5	90	90	90

Table 8 gives data for rats 15, 23 and 7, used in set B of the 30 and 60-day tests. In this table again the first columns are the original learnings; the last columns, the learnings of B in the

60-day test. These rats had received 300 trials in the 30-day test followed by some intermediate training on h. c. If this data were included in the curves, there would be no variation in their essential relations. If anything the interference would be more apparent.

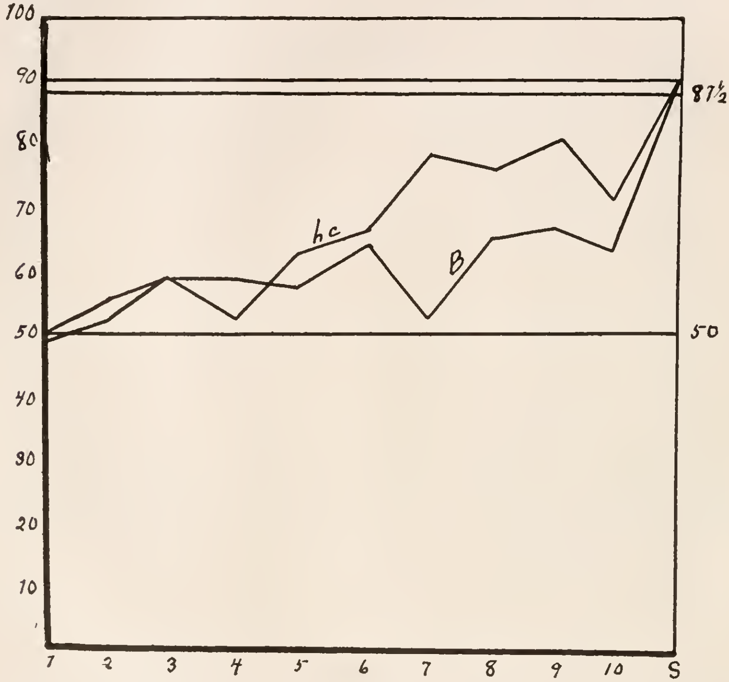

Figure 4.—Relative rates of error elimination in h. c. and in B. Based on rats 15, 23 and 7

The curves in figure 4 begin at essentially the same height and go along together throughout the first six-tenths of the learning. It is during the last four-tenths of the curves that the B-curve remains markedly below that for h. c. (There is no evidence that this was caused by fear.) The interference of the two habits is seen here and in a comparison of the last of h. c. and the first of B. In the average B is no more than a new habit with these rats. Its curve begins no lower than that for h. c. The details are further brought out in table 9, which gives the correct responses in each 10 trials of the first

100 trials of the 30-day test with B. It will be seen from this table that there is no essential difference between the initial stages of the two habits.

TABLE 9

7		15		23	
h. c.	B	h. c.	B.	h. c.	B
5	3	7	3	3	4
3	2	3	5	7	6
3	2	6	7	5	5
5	2	5	8	10	8
2	4	6	5	5	8
4	4	7	5	8	7
4	5	3	5	4	6
7	6	5	7	6	8
6	1	4	7	6	6
3	3	9	8	5	7

IX

Conclusions.—The present paper opens up problems in an all but unexplored field of animal behavior. Keeping in mind the limitations imposed by the number of animals and the type of experiment, the following conclusions may be stated as the more important ones to which our work points:

1. Habit interference occurs in the white rat between a first habit and the formation of a second one.

2. This interference may or may not manifest itself at the beginning of the second habit and may or may not manifest itself later during the second learning.

3. " Interference " is most marked between the end of the perfected habit and the beginning of the new habit. In many cases this may show not genuine interference, but merely the beginning of a new habit.

4. Habit interference may serve greatly to slow up the formation of a new habit. Clear evidence of this forward reference has been found. We have brought to light no evidence that learning the second habit as such interferes with the retention of the first habit.

5. It seems clear that in some cases the lapse of time may be more effective than intervening training in disintegrating a habit.

THE CRITERION OF LEARNING IN EXPERIMENTS WITH THE MAZE

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In comparative studies of the rate of learning in which animals are trained in the maze the selection of a proper criterion by which to judge the progress of habit-formation in different groups of animals offers a rather difficult problem. There can be little doubt that the ability to thread the maze without error is the final test of learning, but whether a single trial without error, three successive trials as used by Hubbert, or a still larger number of errorless runs should be required before the habit is considered as established has so far been determined largely by the convenience of the experimenter. The question is chiefly one of economy of the experimenter's time, but not wholly so, for, although all animals may become automatic in running the maze after long training, an occasional error still appears and no method of evaluating these has been devised.

In some tests dealing with the effects of drugs upon the rate of learning I have recently trained 94 rats in the Watson circular maze, obtaining data which makes possible a limited comparison of such criteria of learning.

The animals were all given five trials per day in the maze with food at the end of each trial. At the beginning of the experiments, as an arbitrary standard of "perfect learning," a single record of three successive errorless trials on the same day was selected. After this degree of proficiency is once attained the animals make very few errors, so that this standard actually represents very nearly the limit of training, but it was chosen simply because it could be attained after about ten days' training.

To test the reliability of this standard in estimations of the difference beween groups of animals its results have been compared with those of another standard, that of the number of trials preceding the first which was made without error. This comparison is best made by correlating the number of trials preceding the first errorless run with the number preceding "perfect learning" for all the animals. The former varied from 10 to 75 with a mean at 23.8±.977, the latter from 10 to 150 with the mean at 47.3±2.99; the correlation in the variations of the two is 0.632±0.061. The coefficient of regression of the variations in trials preceding the first errorless run over those preceding "perfect learning" is 1.304, that of variations in "perfect learning" over first trial is .306. This means that if we are dealing with fairly large numbers of animals and have found a given difference between two groups, as measured by the average number of trials required to make one perfect run, we may expect that the difference in the number of trials required for "perfect learning" will be in the same direction and 1.304 times as great. Conversely, if we know the difference in trials required for "perfect learning" we may predict a difference .306 times as great in the number of trials required for one errorless run.

It follows from this correlation that that group of animals which has made the most rapid progress up to the time when the first errorless run is made will continue in the lead until the limits of training are reached; will, indeed, increase that lead. As a test of the application of this principle, the groups of animals which were treated differentially in the experiments have been graded in the order of the average number of trials required by them to attain to each of the two standards. The results of this are shown in table 1. The different methods of rating result in an interchange in the order of some of the groups but in no case is the position of any one group changed by more than one place.

The groups included in the table are not all strictly comparable. The methods of training were the same in every case but some of the groups differed in the heredity and age of their members, in the season during which they were trained, as well as in certain drugs administration during training. In the separate experiments, all these factors were controlled and the groups *a*, *f*, *g*, and *i*, *c*, and *d* and *b*, *e*, *h*, and *j* are mutually comparable and differ only in the drugs administered. The order of these by the two criteria of learning is—

"P. L."	a f g i:	*c d*:	*b e h j*
1st P. R	a g f i:	*c d*:	*b e h j*

The order is changed in this case only between the groups f and *g*, and the difference between them is not great enough to be significant in either case. There is essential agreement in the results obtained by the two criteria.

As will be noted in the table and from the coefficients of regression, the difference between the groups is greatest when measured by the difficult standard of three perfect trials.[1] Are these differences more significant on this account? At first sight it might seem so. The number of animals considered remains constant and hence, other things being equal, the ratio of the difference to its probable error increases. But the probable errors are dependent also upon the amount of variability and a further analysis of the data shows that the coefficient of variation remains constant or is even increased when the more difficult standard is used. The figures in table 2, which are taken from groups *c* and *d*, illustrate this. The probability that the first difference in the table (3.54) is due merely to chance is about 1/3; that the second (4.12) is due to chance is 1/1 or greater. A glance at the probable errors for the averages of all the rats (page 70) shows that these are quite consistent with the results for the smaller groups.[2] The coefficient of variation in the number of trials preceeding the first errorless run is .5900, for those preceeding " perfect learning " is .6107 and the probable error of the average of the latter is proportionately greater than that of the former . If two such groups were compared by the two criteria the differences obtained would obviously bear the same relation to their probable errors as do those in the smaller groups.

The general results of this analysis point to the following conclusions: 1. Where there is a difference in the average capacity of two groups of animals for habit-formation, the more difficult the problem that they are required to learn the greater will be the apparent difference between the groups in the practice required for learning. 2. With the increasing difficulty of the problem there is an increase in the extent of variation between the members of the same group so that the greater difference between the groups looses its significance through the increase in the probability of chance variation of the averages. 3. Hence there is no advantage, for reliability of results, in prolonged training where the problem is that of a statistical comparison of different groups of animals by a single standard of achievement.

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[1] Some exceptions occur, but this is to be expected from the small number of animals included in the groups.

[2] No great importance could be ascribed to this fact alone as it does not follow that there is any correlation between the variability within the subordinate groups and the variability of all the animals taken together, but the fact that the same results are obtained for both the small and large groups does seem significant.

These conclusions apply only to a specific technique, but one which has been used extensively in studies of the effect of age, sex, distribution of practice, etc., upon the rate of learning. It may be argued that long training permits the comparative study of the rate of learning at different stages of proficiency. This is quite true, but the analysis of learning curves based upon the averages of several animals has contributed remarkably little to our knowledge of the mechanism of learning and in statistical studies of the sort under discussion there is not time for that detailed analysis of the individual behavior of the subjects which is of value in the interpretation of the form of the learning curve. On the other hand the results of studies of the modifiability of the course of learning by environmental factors are for the most part questionable because of the small number of cases upon which they are based. In many cases differences which are smaller than their probable errors have been regarded as significant, seemingly only because they support the hypothese of the writers.

The use of an adequate number of animals is difficult for the reason that the groups to be compared should be trained at the same time to rule out possible seasonal differences, of which we know nothing at present, while only a limited number of animals can be trained by one man at one time. A possible solution of the difficulty is the cooperation of several students upon a single problem but there is not enough data upon the influence of the experimenter's personal equation to permit of this as yet.[3] The alternative seems to be the simplification of the problems presented to the animals so that a greater number may be trained. If the evidence given above can be verified by more extensive data this solution will doubtless prove to be the most satisfactory.

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[3] The use of two or more criteria as in the experiments reported, while reducing the probable errors of the average difference found, removes hereditary and like individual differences from the category of chance variations and places them on an equal footing with the experimental differences (age, sex, or whatever difference is being studied) as the cause of the diverse rates of learning revealed by the experiments.

TABLE 1

The average number of trials required by differentially treated groups before reaching the standards described in the text. The number of animals from which the averages were taken is given at the left and the relative rating of the groups by the two standards on the right.

Group	Number of animals	Trials preceeding "perfect learning"	Trials preceeding 1st perfect runs	Rating by "P. L."	Rating by 1st P. R.
a	9	24.5	14.8	1	2
b	6	30.0	14.3	2	1
c	16	31.0	16.6	3	3
d	16	35.2	19.6	4	5
e	6	42.5	18.0	5	4
f	10	43.5	23.0	6	7
g	10	48.6	20.4	7	6
h	6	65.3	31.3	8	8
i	9	74.4	32.4	9	9
j	6	82.6	43.0	10	10

TABLE 2

Differences between groups *c* and *d* as measured by the two criteria of learning

Group	Trials preceding first errorless run			Trials preceding three successive errorless runs		
	Mean	Probable error	Coef. of Var.	Mean	Probable error	Coef. of Var.
d	19.60	1.480	.448	35.12	5.922	1.000
c	16.06	1.684	.622	31.00	2.428	.464
Difference	3.54±2.263			4.12±6.40		

THE REACTIONS OF DROSOPHILA AMPELOPHILA LOEW TO GRAVITY, CENTRIFUGATION, AND AIR CURRENTS

WILLIAM H. COLE

Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College

No. 288

INTRODUCTION

Geotropism is characteristic of many animals and is often closely correlated with equilibration. The ear in vertebrates and the statocysts in invertebrates are evidently concerned with this reaction. In insects, however, there are no semi-circular canals or statocysts and it has not been proved that the so-called " static " organs (chordotonal, etc.) have to do with geotropism. Some other explanation is therefore to be sought. The experiments here described were carried out with the common fruit-fly, Drosophila ampelophila Loew, for the purpose of determining (1) whether or not it is negatively geotropic; (2) how it responds to centrifugation and air currents; and (3) what mechanism can control these responses.

Carpenter ('05) concluded that gravity acted on Drosophila as a " directive " stimulus only, some " kinetic " stimulation, such as photic or mechanical, being necessary to induce locomotion. If this is true, how will Drosophila react to centrifugal force and air currents under conditions where light and mechanical stimuli are not effective ? This question was suggested by the fact that the flies, without mechanical stimulation, were found to respond negatively to gravity in the dark as well as in the light. If it should be found that Drosophila reacts negatively to centrifugation or to air currents, then it would seem that gravity is a kinetic stimulus as well as a directive one. Another question closely related with this one, which must be considered is, by what means is the stimulus of gravity received?

The work was done under the direction of Professor G. H. Parker, to whom I wish to express my sincere thanks for guidance and suggestions throughout its progress.

EXPERIMENTS

1. *Effect of gravity in the dark.*—The first experiments were carried out in a dark box modelled after the one described by Carpenter, except that no heat screen was used.[1] The glass cylinder employed was 18 cm. long and 4 cm. in diameter, and was marked off by fine ink lines into six regions of equal length, to facilitate locating the flies at the end of the experiments. A small number of flies were put into the cylinder and attracted to the top end by a strong light. Quickly but carefully the cylinder was placed, this end down, inside the box. After a period of one minute the door was opened, the lights turned on and the position of the flies noted. Observations were also made with a single animal, with smaller and larger cylinders of celluloid as well as of glass, but since the results were always the same it is not necessary to describe these modifications in detail.

The results of 58 trials involving 26 different animals showed that an average of 82 per cent went to the uppermost third of the cylinder after it was inverted, that 4.8 per cent remained in the lowest third and that the others stopped creeping in the middle third. The individual readings for those at the top varied from 67 to 92 per cent. In other words the animals reacted negatively to the stimulus of gravity in the dark. Whether or not this response is due entirely to gravity without regard to the mechanical stimulus of turning them over will be considered later.

One of the sets of records in this series of experiments is given in Table I.

2. *Effect of gravity on flies equally illuminated from above and below.*—The dark box was converted into a light box by the introduction of two electric lights, one at each end. These were either carbon-filament lamps of 16 candle power or 15-watt Mazda lamps. As before, the flies were attracted to the top of the cylinder, which was then inverted and placed in the light box.

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[1] Carpenter's heat screen, because of the thinness of the water layer, was probably of no great value in preventing the action of the heat on the flies.

TABLE I

Showing the position of 5 flies in 14 trials, after having been in the dark box one minute. At the beginning all the flies were in section 6. 85.71 per cent crept to the uppermost third of the cylinder (sections 1 and 2).

NUMBER OF FLIES IN THE DIFFERENT SECTIONS OF CYLINDER

Trial number.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Section 1.....	5	4	3	4	4	3	4	4	5	3	2	3	3	4	51
Section 2.....		1	1			1				1	2	1	2		9
Section 3.....				1			1			1	1	1			5
Section 4.....			1		1	1		1						1	5
Section 5.....															0
Section 6.....															0

After one minute the readings were taken. Eighty per cent of the flies used in 50 trials went to the top section, 9 per cent remained at the bottom and 11 per cent went to the middle. Here also the flies responded negatively to gravity.

A set of records from this series is given in Table II.

TABLE II

Showing the position of 5 flies in 14 trials after having been one minute in the light box with equal illumination at top and bottom. 78.57 per cent crept to the uppermost third.

NUMBER OF FLIES IN THE DIFFERENT SECTIONS OF CYLINDER

Trial number.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Section 1.....	3	5	5	2	3	5	3	3	2	4	1	3	2	1	42
Section 2.....				2	1		2	1	1	1	1	1	1	2	13
Section 3.....	1												1	2	4
Section 4.....	1			1					1			1			4
Section 5.....					1			1	1		3		1		7
Section 6.....															

3. *Effect of gravity on flies illuminated either from above or below.*—In order to study the effect of unequal illumination, a

single lamp was used either at the top or the bottom. When the top lamp was lighted 98.5 per cent of the flies went to the top after one minute, the others reaching the middle section. Twenty trials with 12 different animals were made.

With illumination from below 70 trials on 21 flies resulted in 61 per cent going to the uppermost third and 22.5 per cent remaining in the lowest third. Thus when light acts contrary to gravity a smaller number of flies are found at the top. It is interesting to note that the light stimulus, contrary to expectation, did not predominate over gravity. An increase of the light intensity from 16 candle power to 40 made no difference in the results.

A set of records from an experiment in which the light was below the cylinder and therefore acted contrary to gravity is given in Table III.

TABLE III

Showing the position of 5 flies in 14 trials after having been in the light box with a single lamp (15-watt Mazda) below the cylinder; 55.7 per cent crept to the uppermost third.

NUMBER OF FLIES IN THE DIFFERENT SECTIONS OF CYLINDER

Trial number.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Section 1.....	2	2	3	2	1	2	1	3	2	4	2	2	2	1	29
Section 2.....	1	1							3	1	2	1		1	10
Section 3.....		1	1	2		1					1				6
Section 4.....					2	1	1							1	5
Section 5.....	1	1			1		1	1					2	1	8
Section 6.....	1		1	1	1	1	2	1				2	1	1	12

These results corroborate previous work on this subject in so far as a negative response to gravity is concerned. But in this, as well as in all previous work, mechanical or light stimuli have been operating. The former cannot be eliminated in such experiments since it is impossible to invert the cylinder without moving it. Consequently I next tried a series of centrifuging experiments in which these two kinds of stimuli could be neglected. So far as I am aware the effect of centrifugal force on Drosophila has never before been studied.

4. *Effect of centrifugation.*—The centrifuge consisted of a table mounted on a base capable of revolving, on a fixed axis in a horizontal plane. A small water motor attached to an ordinary faucet furnished the motive power. On the table could be fastened glass tubes of various lengths and bores. In these tubes, the ends of which were tightly corked, one or more flies were placed in the desired position; the tube was then revolved about its middle point as a center at a known speed, the time of revolution usually being one minute.

In the preliminary trials it was found that at a certain speed the flies in the ends of the tube crept toward the center and remained there. If the speed was greatly increased, they were thrown out to the ends. It became necessary therefore to determine the maximum and minimum limits within which a definite response could be noted. The calculation was made according to the formula, $F = \frac{mv^2}{r}$, where F represents the centrifugal force, m the mass, v the velocity of revolution and r the radius. Experiments showed that when F was equivalent to gravity the flies began creeping toward the center. When it was considerably larger than gravity the flies were thrown out to the ends. Furthermore when F was just equivalent to gravity the flies crept toward the center until they reached a point where the force was less than gravity, the speed remaining the same. To induce further creeping toward the center the speed had to be increased, since the shorter the radius of revolution the greater the speed necessary to generate the same force.

The tube ordinarily used was 50 cm. long with a diameter of 2 cm. Applying the formula, $n = \frac{980}{4\pi^2 r}$, which can be derived from the previous one, the speed necessary to generate a force equivalent to gravity is easily calculated. When the flies are in the ends of the tube, therefore, it must revolve approximately once every second; as they move toward the center the speed must be gradually increased. But since the flies can creep against a force much greater than gravity without losing their equilibrium, a constant speed can be found at which they will creep all the way to the center. This is about 85 revolutions per minute. Experiments carried out in darkness, in diffuse daylight, and with a bright light at one side all gave similar results. A check experiment, in which the speed of revolution was very low (from 1 to 40), showed the flies creeping about indifferently; therefore it was concluded that mechanical and light stimuli did not affect the response in these experiments.

One hundred trials with 40 different animals, under the various conditions described above, showed that a speed of 60 revolutions per minute was necessary to start them moving toward the center. As the flies approached the center the speed had to be gradually increased in order to keep them moving toward the center. At a distance of 2 cm. from the center a speed of approximately 210 revolutions per minute was necessary to accomplish this. At a distance of 25 cm. from the center any speed greater than 100 revolutions per minute mechanically prevented the flies from creeping toward the center. Table IV gives the data for several trials taken at random from the series of 100.

TABLE IV

Showing the position of 14 flies in 8 trials after one minute of revolution at different speeds.

Number of flies	Position at beginning	Number revolutions per min.	Time of revolution	Position at end of experiment
2	End	50	1 min.	End
2	End	72	1 min.	½ way from end
1	End	90	1 min.	Center
1	¾ way from end	120	1 min.	End
2	¼ way from end	72	1 min.	¾ way from end
2	½ way from end	96	1 min.	Center
3	End	100	1 min.	End
1	2 cm. from center	210	1 min.	End

These experiments demonstrate a very definite response and prove that Drosophila reacts negatively to a centrifugal force equal to or slightly greater than gravity, as well as to a gravitational one, without regard to other stimuli. We may therefore consider gravity a kinetic stimulus as well as a directive one.

5. *Effect of air currents.*—The next question considered was, How does Drosophila respond to air currents? Horizontal, upward, and downward currents, produced by an electric fan, were directed into a glass cylinder like the one used in the dark box. Their strengths were so adjusted that the flies did not lose their equilibrium.

(a) *Horizontal currents.*—These trials, carried out in diffuse daylight, did not give as definite a response as could be desired. The flies were liberated singly from the bottle containers at the open end of the cylinder, and their course of locomotion noted. In only 11 trials out of the 40 made, could the response be called definite. In 7 of these the flies crept against the current, in 2 they crept against it for about 10 cm. and then flew with it, and in the other 2 they flew with the current. Every case of creeping was against the current and every case of flying was with the current. In the control experiments with no air currents the flies crept or flew in any direction.

(b) *Upward vertical current.*—In these trials 29.5 per cent of the flies crept upward with the current, 59 per cent flew upward, and 11.5 per cent crept downward. Gravity is here acting contrary to the force of the current and the 29.5 per cent creeping up is probably a purely negative geotropic response. The creeping downward was very slow and intermittent. The largest number (59 per cent) flew with the current.

(c) *Downward vertical current.*—The results of 61 trials showed that 27.8 per cent of the flies crept upward against the current, 23.2 per cent flew upward, while 49 per cent flew downward with the current. An interesting observation was that practically all the flies crept upward a short distance before carrying out the main response. In the control experiments, with no air current and the cylinder in a vertical position, the only reaction that could be noted was a negative geotropic one, the other movements being indifferent.

There is therefore a tendency for Drosophila to fly with the air current, a positive response, and to creep against the current, a negative response. Since there were extremely few flying responses in the experiments with gravity and centrifugal force, no comparisons can be made with them. But the creeping against the currents corresponds with the negative response to gravity and centrifugation.

DISCUSSION

The responses, other than mechanical ones, of animals to centrifugal force and air currents have not been thoroughly investigated. Only a few references to centrifuging experiments are found in the literature. Loeb ('91) stated that Cucumaria cucumis responds to centrifugation by contracting its body and remaining motionless. This condition persists for from one-quarter to one-half an hour afterward, when crawling is begun again. Although he studied the geotropic reactions of certain caterpillars, ephemerid larvae, coccinellids and blattids, no reference is made to testing the effect of centrifugal force on them.

Jensen ('93), having found that Paramoecium was negatively geotropic, discovered that it moved centripetally with weak centrifugation. Davenport and Perkins ('97), after concluding that "gravity acts as an irritant to which the organism makes a response, belonging to the category of adaptive responses," say that this irritating pressure "may be replaced by a centrifugal pressure, when the same geotactic orientation will occur." Harper ('11) also reported that Paramoecium reacted negatively with weak centrifugation. He believes, however, that "the response of Paramoecium to gravity is a purely mechanical tropism."

On the other hand, geotropism of animals has been extensively studied, and many theories put forth for its explanation. It is generally accepted that the ear or some "static" organ controls this tropism in certain forms. But for insects there is much doubt as to how the stimulus is received. Kafka ('14) reviews this question and summarizes the different theories, as follows: Loeb believes that the chordotonal organs at the base of the halteres of some Diptera are the organs of reception. Pflügstaedt and Weinland describe other structures which might serve as sense organs. Similar organs have been described by Hochreuther for Dytiscus, by Janet for Hymenoptera, and by Baunacke for nepid larvae. But conclusive proof that any of these organs, the functions of which are little understood, control the response to gravity is entirely lacking.

The reactions to the three kinds of forces described above suggest an explanation as to how the stimuli are received. When the fly is creeping upward against gravity the weight of the body is on the legs. There is, therefore, a tension on the leg muscles distinct from that caused by creeping. When a fly is creeping against centrifugal force a similar tension of the leg muscles is produced. Furthermore, creeping against an air current causes the same kind of tension. Very probably, then, the stimuli in all three cases are due to this tension and are received by the sensory nerves of the leg muscles, the response being an attempt to preserve the equilibrium of the body. Negative geotropism in Drosophila, then, is concerned with the muscle sense. Radl ('05) expressed the view that the insect muscles are capable of acting as special sense organs when he wrote "das Gehör der Insekten ist ein verfeinertes Muskelgefühl."

The flying response does not fit into this explanation and it may be that it is not influenced at all by gravity. It is a matter of common observation that the house flies on a brightly illuminated window usually *creep* upward but fly in all directions. The flying is much more indefinite than the creeping. In my observations on geotropism only a very few cases of flying (about 3 per cent) were seen. Cylinders with a diameter as large as 12 cm. were used so as to allow flying, but no greater proportion of cases was seen than in the smaller cylinders. When disturbed the animals flew about indifferently for a short time and then, after alighting, continued their upward creeping. In the centrifuging experiments no flying at all was seen. The air currents often caused flying, and in the large percentage of cases the animals flew with the current, although they were able to withstand it. It seems therefore that the response to gravity is much less marked in flying than in creeping, where it is very definite.

CONCLUSIONS

1. Drosophila ampelophila Loew, when creeping, reacts negatively to gravity, to a centrifugal force which is equal to or slightly greater than gravity, and to air currents without regard to other stimuli. Gravity is, then, a kinetic as well as a directive stimulus.

2. The stimuli causing these reactions are probably received by the sensory nerves of the leg muscles.

3. It is probable that flying reactions of Drosophila are not influenced by gravity.

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GEOTROPISM IN PLANARIA MACULATA

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Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College

No. 289

Flat-worms, such as planarians, are commonly collected from the *underside* of stones in a stream or pond (Bardeen, '01; Pearl, '03; Whitehouse, '14). The resting position of these animals, with their ventral surfaces uppermost, would seem to indicate a negative response to gravity, since when moving they may be in any position, depending upon the particular surface over which they happen to be gliding. This investigation has as its object the analysis of the resting behavior of these worms. The specimens used were Planaria maculata Leidy and were taken from Fresh Pond, Cambridge, Mass. A stock was brought into the laboratory and kept in a large jar on a table about four feet from a north window.

To ascertain the relative importance of light and gravity in the reactions to be studied, an experiment in the following form was carried out. One-half of one surface of a glass plate, 10 x 8 cm., was coated with black wax. This plate was supported in a horizontal position by wax feet 4 mm. high on a second glass plate. The pair were placed in a flat dish and covered with water to the depth of 3 cm. The flat dish had a collar of black paper about its sides, so that only light from above could fall on the plates. Then twenty planarians were placed at one time on the upper plate, at another on the lower one, and their positions recorded twice a day. As the animals moved about over the whole dish for an hour or more after beginning the experiment, the fact that they had started from the upper or lower plate was not significant.

The results of 30 readings showed that 30 per cent were not under the plates, but usually in the shadow near the angle between the bottom and side of the dish, 70 per cent being found between the plates, and always under the black half. Of the latter, one-fifth were on the under side of the upper plate (ventral surface up), and four-fifths on the lower plate (dorsal surface up).

Since, as the preceding experiment showed, the influence of light was so marked, it was decided to eliminate this factor by conducting all the subsequent experiments in a light-proof box. To eliminate thigmotropism and to provide a continuous surface which should have all possible relations to gravity, spherical balloon flasks were used. These flasks were 13 cm. in diameter. They had a short neck 4 cm. long. Three regions of equal area were marked off on the surface of each flask, a ring about its equator and a segment at either pole. These three regions were designated top, middle, and bottom. The flasks were so marked that in one the neck came in the top, in another in the middle, etc. In the experiments very few worms lodged in the neck and the per cent of such was practically the same whether it occurred in flasks with the neck in the top area, in the middle, or in the bottom. In the tabulation of results worms in the neck are not included.

Twenty worms were used in each experiment. Readings of their positions were made at 9 A. M., 1. P. M. and 4. 30 P. M. In a few cases readings were taken at intervals of two hours, but even then the animals were at rest. They were made to start moving before being returned to the box, as a means of redistributing them for the beginning of another trial. It was found that the positions of the planarians in the flasks changed greatly during the first few days after being put into the dark. At first the majority were to be found in the bottom of the flasks. A few days later they were equally distributed in the three areas. When they were fed there was a sudden departure from this equal distribution and the majority would be found in the top. They again distributed themselves equally in the three areas three or four days after feeding. Table I gives a summary of results. The numbers are the per cents taken from 10 or more readings. By " from light " is meant worms taken from the stock which had been kept in the light. " From dark " means worms which had been in the dark-box for a week or longer. " Fed " worms are those which were fed on liver on the day of the experiment or every other day during experimentation. "Unfed" are those which had been without food for five days or more.

From these results it is evident that two factors are concerned in the distribution of the worms: First, previous history as regards exposure to light, and second, the state of metabolism of the worms in relation to feeding. Both fed and unfed worms which had previously been in the light were found to be mostly positively geotropic immediately after being put in the dark. The fed ones then became negative for a short time. Finally both became indifferent if feeding was stopped. Those which had been in the dark for a long time were negative when fed and indifferent when unfed. Walter ('08) makes the statement that Planaria gonocephala "seems, after several hours of exposure to the dark, to be positively geotropic," while Kafka ('14, p. 151) says that Planaria gonocephala is negatively geotropic after long retention in the dark. Both of these apparently contradictory statements are probably true, since the *length* of exposure to the dark may very well be an important factor in the geotropism of Planaria gonocephala, as my experiments show for its close relative, P. maculata.

That this negative geotropism of fed worms in the dark is not in reality a response to oxygen from the open neck is shown by the following experiment. A flask containing 20 planarians was completely filled with water, and the mouth covered by a glass plate. It was then immersed neck downwards in a jar of water in the dark-box. Previous to the experiment the planarians had been fed every other day for two weeks, and were dividing so that at the end of the experiment there were 27 worms instead of 20. The per cents found in the three areas of the flask under these conditions were as follows: Top, 58; middle, 33; and bottom, 9. These are of the same order as the last two series of the per cents given in Table I. Table II shows this relationship.

TABLE I

			Area of the Flask			Month
			Top	Middle	Bottom	
From light	Unfed	1st 2 days in box...	19	10	71	Nov.
		1st 2 days in box...	17	21	62	Jan.
		5+days in box.....	38	24	38	Nov.-Jan.
	Fed before expt.	1st 2 days in box...	16	21	63	Nov.
		3rd, 4th days in box.	63	21	16	Nov.
		5th day onward...	36	23	41	Nov.
From dark	Unfed	....	36	30	34	Nov.
		....	38	35	27	Dec.
		....	35	36	29	Jan.
	Fed contin-uously	....	58	28	14	Dec.
		....	68	26	6	Jan.

TABLE II

		Area of Flask			Month
		Top	Middle	Bottom	
From dark and fed	Flask open to air..........	58	28	14	Dec.
		68	26	6	Jan.
	Flask submerged in water...	58	33	9	Jan.

Table II shows that the per cents were the same whether the flasks were open to the air or entirely submerged in water. If the worms had been responding to oxygen and not to gravity, we should expect in this experiment to have found them in the bottom near the mouth, where oxygenated water could enter from the jar outside. They were actually found in the region farthest from the supply of oxygen, so that their position was a true response to gravity.

To find whether the presence of the slime tracks influenced this behavior, indifferent animals were kept for a week (1) with no change of water, but the slime washed out from the flask daily, (2) with change of water daily, but the slime not washed out, and (3) with no change of water and no cleansing of the flask. Table III gives a summary of results.

TABLE III

		Area of Flask		
		Top	Middle	Bottom
Unfed and from dark.	Slime washed out daily.......	44	30	26
	Water changed daily.........	29	31	40
	No washing or change of water	35	26	29

Since the planarians remained practically as indifferent to gravity throughout the experiment as they were before it was begun, the presence or absence of slime tracks probably had little effect on their geotropism.

The results of these experiments are in line with observations on the stock animals. They usually remain in the shadow under the stones and along the side of the dish. The majority rest on the underside of the stones, but a great many are to be found on the sides of the dish. Immediately after they finish feeding, they glide to the top and move about over the dish. If the water is changed at this time they soon come to rest near the bottom again. If the water is allowed to get foul after feeding, they remain at the top, probably in this case on account of lack of oxygen below. I have been unable to see daily migration such as Walter ('08) observed.

It would seem reasonable, therefore, to suppose that the collector who finds planarians ventral surface up on the underside of rocks, sees those which have been feeding, while if he looked in other places he might find the unfed ones in any position.

Since Planaria maculata has no otocyst, it may be that after eating, the food in the digestive tract serves as an otolith, and after digestion and assimilation the animal becomes indifferent to gravity because the food is no longer able to press upon the digestive epithelium. This does not account for the fact that fed worms are positively geotropic when first put in the dark.

I wish to thank Dr. Parker for suggesting the problem and for advice as to methods.

CONCLUSIONS

1. Unfed Planaria maculata which have been in the light are positively geotropic when first placed in the dark. After several days in the dark they become indifferent to gravity.
2. Fed Planaria maculata which have been kept in the light are likewise positively geotropic at first. But they become negative after two days and indifferent after five days.
3. Fed planarians which have been in the dark for some time are negatively geotropic.
4. The presence or absence of slime tracks has no influence on the geotropism of these planarians.

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THE DELAYED REACTION WITH SOUND AND LIGHT IN CATS

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I

The experiments herein reported on the delayed reaction in cats were carried out during the session 1915-16 in the Psychological Laboratory of the University of Texas under the direction of Prof. W. S. Hunter. The purpose of the work was: first, to determine the limits of the period of delay; second, to ascertain definitely the behavior during delay; and third, to describe as nearly as possible the method of reaction which leads to success. Careful records were kept of the behavior during the period of delay, and particularly of the bodily attitudes maintained and of the orientations. Associations were set up between movements that led to food and a light or buzzer, as the case might be, which could be in either of three boxes. With this association well established, tests were instituted in which the stimulus was cut off before the reaction was completed. And throughout the remaining experiments the subject had to respond in the absence of the stimulus that until now had been present at the moment of response.

It was my purpose to use in this problem a method of procedure sufficiently similar to those already used with other animals,—raccoons, rats, dogs, and children—that by comparison the relative ranking of the cat in the solution of the problem could be ascertained.

II

1. *Cats tested on light.*—The four cats used in these tests were Jim ♂, Tom ♂, Fay ♀, and Bobby ♀. Jim and Bobby were both about ten months old, vigorous, healthy animals, and their records may be accepted as typical. The other two were young cats that had not been properly cared for. They were weak and died before they were well into the experiments.

2. *Cats tested on sound.*—Four cats were used in the tests on sound. Bess ♀ and Phil ♂ were each about two years old. Judy ♀ was about one year and Kitty ♀ at least two years old. Bess and Phil continued strong and did excellent work throughout the experiments. Judy and Kitty, on the other hand, died early in the work. From this it is seen that four cats were at work practically all the time,—two on the light tests and two on the sound tests.

One would think from the number of deaths reported that the cats were in poor physical condition. Such, however, was not the case. Their general health was very good. Those that died did not experience a long period of sickness, but died within thirty-six hours of the appearance of distress. There was only one exception to this, and in this case the cat was replaced by another rather than risk her recovery.

It was much more difficult than I had expected for them to become physically adjusted to their new environment. They were kept in a wire cage 12′ by 3½′ by 6′ high, in a room adjacent to the experiment room. Their room was well ventilated, and a large east window provided an inlet to the morning sunshine. The difficult thing was to find the most nourishing food for them. Milk, with a small amount of raw steak, proved to be the most satisfactory.

III

DESCRIPTION OF APPARATUS AND METHODS

In Fig. 1 is shown the ground plan of the box used. The box was made of ¼″ boards and was 26″ high, with the doors at a, b, c, 10″ high by 7″ wide. The distance between these doors was respectively 20″, and the distance from the release door E to each of the doors was 44″. The door E of the release box was raised by a cord passed over a pulley directly above it and 6½′ above the floor of the apparatus. Besides this pulley were three other pulleys through which passed cords from the three sliding doors marked D in the figure. With the aid of these cords, the experimenter could stand behind the release box and control the door at each of the boxes. The release box was covered with wire of ½″ mesh, and the board B upon which was fastened the switches for both light and sound. The light stimulus came from 8 c.p. lamps, so wired that any one of them could be cut in at a time. The current was obtained from a 110 volt switchboard B.

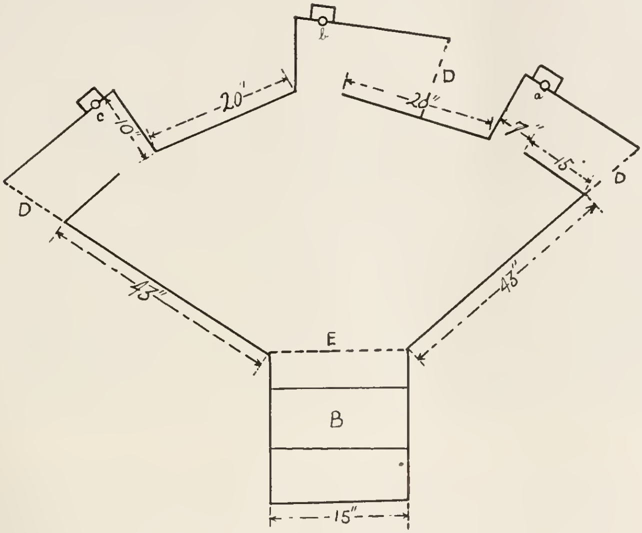

FIGURE 1.—Ground plan of apparatus

In order that the cat might not come in contact with the lamps, and, also, not be hindered in entering the boxes, a hole was bored in the back wall of each of the boxes and a lamp placed outside and behind each box. The holes were of the same size and 5″ from the floor. The lamps were mounted on bases which rested on the floor, and were placed behind the holes so that they had equal intensities and could be observed with equal ease from the release box. One 8 c.p. lamp hung over the center of the apparatus and 4′ from the floor throughout the experiment. This light was shaded with a paper bag which made it necessary to keep fresh sawdust on the floor of the box to make the movements of the animals clearly visible. At the outset I was compelled to cover the entire apparatus, as the cats were free to jump out at will. The wire used for this purpose was of $\frac{1}{2}''$ mesh and its tendency to blurr the field of vision made it still more necessary that the white sawdust be used.

Fig. 2 should give a clear presentation of the essentials of the box when taken in connection with Fig. 1.

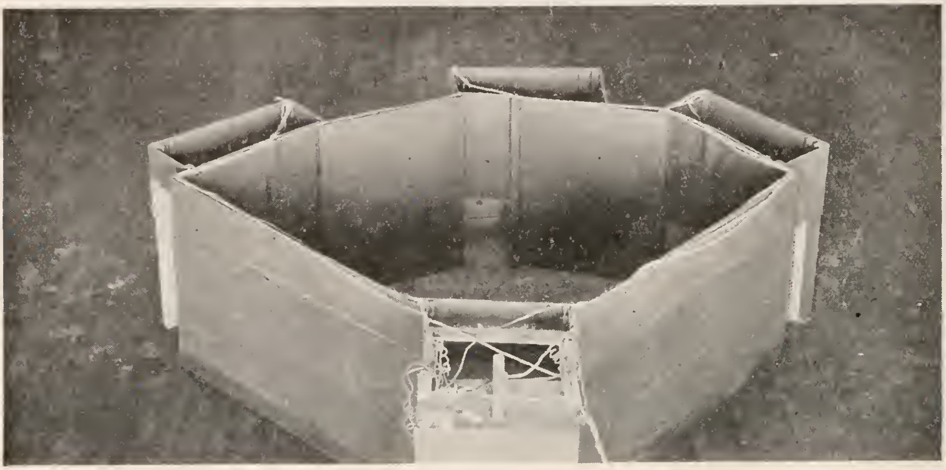

FIGURE 2

The cats on sound used the same apparatus as those on light, the only difference being the change in stimulus. On the switchboard B, Fig. 1, were placed three buttons which corresponded to each of the three light boxes, a, b, and c. In each of these boxes a buzzer was suspended directly over the door and 12″ from the floor of the apparatus. These buzzers were suspended by a coiled wire, and were not in contact with the apparatus. The system of wiring was the same as that of lighting—i.e., any buzzer could be sounded at the wish of the experimenter by pushing the proper button on the switchboard B. Such an arrangement made it possible for the experiments on both sound and light to be carried on without any interference. So far as the knowledge of the experimenter goes, the cats on light never found the buzzers, nor did the cats on sound find the lamps.

The general method of experimentation was as follows: The animal to be tested was put in the release box which is shown in Fig. 1. Now, suppose, for example, that the lighted box were the one on the left, c; its exit door would be opened and its light turned on. When the experimenter was sure that the cat had seen the light or heard the sound, the animal was released. A careful, detailed record was kept of the direction in which the animal was oriented at the moment of release and its path to the exit. Any unusually wide turn in the path was always recorded. Hesitation and zig-zag movements were especially noted whenever and wherever they appeared in the cat's response. In these experiments the cats should go straight to the lighted box, and through its exit door and back to the entrance of the release box where they got food. With the cats on the sound problem, the reactions were the same. With them, however, the " lighted " box was a " sound " box.

When the cats were sufficiently trained to choose the stimulus box (lighted or sounded, as the case may be) almost perfectly, delays were begun. The periods of delay were much the same as those used by Hunter.[1] The first delay was to turn the stimulus off just as the animal reached the box. In the second delay, the stimulus was cut off when the animal was half way to the box. In the third delay, the stimulus was stopped just as the animal made its first move in response after the door of the release box was raised. And, in the fourth delay, the stimulus was cut off just before the door of the release box was raised. In this fourth stage a genuine delay first enters in. The first three stages of delay were of little or no value as delays. Their primary purpose was to bridge over the period of stimulus to non-stimulus, to bridge that period between acting in the presence of a stimulus and acting in the absence of a stimulus. All that was necessary to make a correct response was, in each case, for the cat to continue in the direction he was going. There was no further choice to be made. The fourth delay, however, was genuine, although of small duration. *The stimulus was cut off before the cats were released.* Throughout the remainder of the experiments the cats were compelled to react in the absence of the stimulus that until now had been present at the moment of response.

There was no definite standard adopted by which to promote from one period of delay to another. The general method used, however, was to promote the animal as fast as possible, and only demote when the records showed him unable to bridge the delay. There were no special arrangements made for punishment in case of error. It was easy to observe, however, that there was a certain degree of punishment following each error. These punishments were: having to back out of a box, and having food and freedom deferred for a longer period of time. Although the cats were expected to go straight to the stimulus box, no wide turn in their pathway is recorded wrong unless they approached the entrance to one of the other boxes. The apparatus was so constructed that the animal could not see the position of an exit door, i.e., whether it was open or closed, without actually approaching the particular box.

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[1] Hunter, Walter S. The delayed reaction in animals and children. *Behav. Mon.*, vol. 2, no. 1, 1913.

IV

EXPERIMENTAL RESULTS

1. Three Compartment Experiments

A. *Learning the association.*—Although the primary purpose of this investigation is a study of the delayed reaction proper, it is well to make additional note of the learning process. Table I gives the number of trials required by the cats of set A to learn the association between the light and the getting of food. Each cat was given 10 trials daily. Fay, the last reported in the table, died at the end of 50 trials. Her results are reported, however, because 75% of her last 20 trials were successful.

TABLE I

Cats Tested on Light

Cat	Number of trials	Number correct	Per cent correct	Number correct of last 50	Per cent correct of last 50
Bobby..............	130	96	73	47	94
Jim.................	110	84	76	49	99
Tom................	170	112	65	45	90
Fay.................	50	25	50	25	50

The number of trials required by the cats on sound, set B, are given in table II. The last cat reported in this table died at the end of 40 trials. For this reason no record of her work appears in the last two columns of the table.

TABLE II

CATS TESTED ON SOUND

Cat	Number of trials	Number correct	Per cent correct	Number correct of last 50	Per cent correct of last 50
Bess	180	123	68	43	86
Phil	70	44	63	37	74
Kitty	110	68	61	32	64
Judy	40	26	65	..	..

These results indicate, first, that the cats of each set learned the association readily. The learning curve would appear short and steep. And, second, they indicate that it is more difficult to maintain a high efficiency in set B than in set A. This is indicated by the fact that, while Bess and Phil, both of set B, made 86% and 74% respectively correct in the last 50 trials, Bobby and Jim, of set A, made 94% and 99%.

Although the differences of results, as given in the tables above, are not conclusive, the experimenter is of the opinion that the sound tests present the more difficult problem. These variations may well be explained on the basis of individual differences, but it is to be noted that the animals tested on light have the better records. This probable increase in difficulty in the sound tests is due, no doubt, to the timidity on the part of the cats when approaching the sound. The records show, as is indicated in the next paragraph, that the cats were for some time rather frightened by the sound of the buzzers. This caused an increase in the number of errors and so a decrease in the percentage of correct reactions. Before a definite conclusion can be reached a sufficient number of cats, to eliminate errors from individual variations, must be tested.

Observations of the behavior of the animals during the learning period on sound, which were recorded from day to day, suggest several smaller divisions. (1) A period of disregard. My notes read, " Bess appears to give no attention to the buzzer," and, again, the next day, " Bess walks about freely without noticing the buzzer." (2) A period of disturbance. This period may be characterized by a behavior which may be termed " awareness " or " worry." The cat stops, turns head, looks, and calls as if in danger. This note is recorded, " Bess dislikes to go to the sound. She appears shy and afraid of the buzzer. She will venture to the door, stop, and squat; look up at the buzzer and sometimes rise up and ' sniff ' at it before going into the box." (3) A period of hesitation. The behavior of this period is characterized by wavering and by starts and stops. And, in period (4), the cat gives strict attention to the stimuli. Here the behavior becomes more nearly perfect, the path of reaction has been made straight, and the percentage of correct reaction is high. With the animals tested on light, set A, the same learning period divisions could be made. In this case, however, the period of disturbance was not accompanied by so much timidity and fear.

During this period of experimentation all possible care was taken to prevent any preference for particular boxes. Should such a tendency be observed, control tests were given to break it up before the position habit was well developed. At the end of the first 60 trials each box had been presented 20 times, and the records show that no box was chosen more than 26, nor less than 16 times by any one of the eight subjects.

For comparison we bring together in table III data on learning the association obtained by Hunter in his study of animals and place beside it that of our own subjects.

It is of interest to note that all the cats fall in the class with Bob, Hunter's most rapid raccoon. Bob learned the association in 120 trials while the eight cats used in these tests ranged from 50 to 180 trials with an average of 107 trials each. The curve representing the learning period for the discrimination of the three compartments was very short and steep, yet broken and irregular. With continued practice, this irregularity would undoubtedly have been eliminated; and the cats of each set would have attained perfect mastery of their problem.

TABLE III

	Number of trials on learning		Number of trials on learning
Raccoons—		Rats—	
Bob	120	No. 9	280
Betty	340	No. 12	440
Jack	540	No. 13	250
Jill	825	No. 15	220
		No. 16	480
Dogs—			
Blackie	560		
Brownie	650		

TABLE III—*Continued*

	Number of trials on learning		Number of trials on learning
		Cats—	
		Bobby	130
Rats—		Jim	110
No. 2	176	Tom	170
No. 4	175	Fay	50
No. 5	505	Bess	180
No. 6	800	Phil	70
No. 7	361	Kitty	110

(c) *Controls used.*—In the construction of the apparatus, every effort was made to eliminate all possible differences in the compartments which could be used as guides to correct reactions. The backgrounds surrounding the entrances to the compartments were all alike painted black. Since the backgrounds were all of the same brightness, and, since everything remained constant with the single exception of the exit doors to the compartments, controls were put in to determine their possible effect. In order to test this, the three doors were all opened and the tests were given by the usual method under conditions in all other respects normal. The results were entirely negative. In no case did an animal make use of the doors as cues to its reactions.

Again, control tests were introduced to determine whether or not the animals were really depending upon the applied stimuli (light or sound) for cues for guiding their reactions. To test this, experiments were made under normal conditions except that each time the stimulus (sound or light) was withheld .30% correct reactions was the highest made by any subject under these conditions. It is clear, therefore, that normally the reactions were made either to sound or to light.

Not being able to secure the same pitch and intensity in each of the three buzzers, control tests were made to determine whether the animals had formed associations between them on the basis of quality. The buzzers were all interchanged—buzzer *a* took the place of *b*, *b* the place of *c*, and *c* the place of *a*. No case was found where the differences in pitch and intensity were used as cues for reaction. These qualitative differences could well have been effective during the period of learning the association; but, on the delayed experiments, they could be of little or no value. The essential cues in handling delays must be factors that are variable from trial to trial otherwise they cannot be selective in nature.

No temperature controls were used. They were thought to be unnecessary because of the following: 1. The lights were turned on but for a short time. 2. They were outside of the main apparatus. 3. The cats oriented immediately when the lights were turned on and reacted precipitately when released. And, 4, the behavior of the cats on light was the same as that of those on sound where temperature could not be involved.

B. *"Delayed" experiments.*—Since in the first four delays used the entire reaction was not performed after the stimulus had been removed, it is probable that they should not be termed delays at all. The stimulus was always continued until the experimenter was convinced from all external evidence that the cat had become aware of its presence.

The cats tested on sound and those on light were all presented their problems by the method described above, but for convenience the data will be discussed separately.

(a) *Set A* (*cats tested on light*).—

Delay I.—In delay I the light was turned off just as the cat reached the correct compartment. Bobby was given 30, Jim, 20 trials; and for both of them each trial was successful. With the association well established, the turning off of the stimulus at this point in the reaction effects no change in their percentage of correct response.

Delay II.—In this delay the stimulus was cut off when the cat was half way from the release box to the correct compartment.[2] Jim was given 10 trials with all of them correct. Bobby was given 60 trials with 56 correct. There appears to be no difficulty in making the step from delay I to delay II, even though the cats here made one-half of the distance of response in the absence of the stimulus. After the cat is well set out, then, on his reaction, the stimulus may be withdrawn without affecting the response.

Delay III.—The only difference in this delay and number II is that here the stimulus is withdrawn before the cat is well on his way, while in II the reaction was half completed. Jim was given 20 trials all of which were correct. Bobby was given 60 trials with 57 correct. The reader will notice that the cats have still met no difficulty.

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[2] In case the cat started from the release box in a different direction from that of the stimulus, e.g., if he started toward c when the stimulus was at a, the stimulus was not turned off until he did turn in the direction of the stimulus compartment, and so in this case, was well on his way.

Delay IV.—Bobby was given 80 trials of which 66, or 82%, were correct. Jim received 130 trials, 107 of which were correct, making also 82%. Here the first difficulty of bridging over a period of delay appears. The door of the release box and the cutting off of the stimulus were operated simultaneously and without reference to where the cat was or what it was doing. Thus the animal was forced to initiate the reaction and perhaps make a choice of compartments, in the absence of the stimulus. The data show that Jim took much longer to master this delay than did Bobby, although he had held a higher percentage on fewer trials in the three preceding delays. The fact that Jim had received 100 trials less than Bobby in these preceding delays can be offered as explanation of his need of 60 more trials here. It seems natural that had he not been advanced so rapidly from one delay to another he would have been better prepared for this new delay, and, being better prepared, would have bridged over it much more quickly.

Two seconds delay.—At this point in the experiments a metronome was placed in an adjacent room to mark the period of delay in seconds. At this distance its sounds could be easily heard by the experimenter, yet they were not thought to be strong enough to distract the attention of the animals.

Bobby was given 130 trials with 106, or 81% correct; while Jim was given 200 trials, 143, or 71% of which were correct. Of the last 40% of Bobbie's trials, 34, or 85% were correct; of the last 40% of Jim's trials, 32, or 80% were correct. The data do not show that the reactions were poor at the beginning of the delay and grew better with successive trials, but rather show an irregularity throughout. Bobby, e.g., was perfect on the first 10 trials, while after having received 70 trials she made only 50% on 10 trials. Again, Jim, after 160 trials, made only 30% on 10 trials, yet on the 10 just preceding, he made 90% and 80% on the 10 immediately following.

Four seconds delay.—In the four seconds delay experiment, 180 trials were given Bobby with 141 correct, and 150 given Jim with 118 correct. Each made 78% correct. Jim's last 30 trials showed much improvement, 29 of them being correct reactions. Although Bobby had 30 more trials on this delay than Jim, she made only 26 out of her last 30 trials. This is readily explained in the light of the fact that the middle compartment was dropped out during this period with Jim, while Bobby continued on three compartments. Jim had made 70% on the last 40 trials preceding the 30 trials mentioned above, of which he got 29 correct. At the end of these 40 trials, the middle compartment was dropped out. Of the first 10 trials with only two compartments, Jim made 100% correct. The records show that Jim would have made a higher percentage than 70 much sooner had it not been for a tendency to drop out the middle box. This is not only seen in table IV, but by the fact that when he received the stimulus only from boxes "a" and "c" (the experimenter having dropped out the middle box), he made 100% on the first 10 trials.

TABLE IV

Daily Record on 4 Seconds Delay with Light

Cat	Number of trials	Number correct	Distribution of errors a	b	c
Bobbie.........	10	6	1	2	1
	10	9	0	1	0
	10	10	0	0	0
	10	7	2	0	1
	10	7	2	0	1
	10	8	0	2	0
	10	8	0	2	0
	10	7	1	1	1
	10	8	0	2	0
	10	8	0	1	1
	10	8	0	2	0
	10	7	1	2	0
	10	7	1	1	1
	10	8	0	2	0
	10	8	1	1	0
	10	9	1	0	0
	10	9	0	0	1
	10	9	1	0	0
			11	19	7
Jim...........	10	9	0	1	0
	10	8	0	2	0
	10	7	0	2	1
	10	6	0	3	1
	10	7	0	3	0
	10	7	0	2	1
	10	8	0	2	0

TABLE IV—*Continued*

Cat	Number of trials	Number correct	Distribution of errors		
			a	b	c
Jim...........	10	9	0	1	0
	10	7	0	3	0
	10	7	0	3	0
	10	7	0	3	0
	10	*7	0	3	0
	10	10	0	0	0
	10	9	1	0	0
	10	10	0	0	0
			1	28	3

Six seconds delay.—Bobby was the only cat either on light or sound that was tested on the six seconds delay before the middle box was taken out. Although she had made 85% on her last 40 trials on the four seconds delay, she fell to 50% on the first 10 trials in the six seconds delay. After 90 trials with only 50% of the last 40 correct, she was put back on the four seconds delay where she was given 70 trials, making 80% on the last 50. She was again given 20 trials on the six seconds delay with 55% correct. After 60 more trials on the four seconds delay with 85% correct, she was given 20 trials on the six seconds delay with 70% correct. The records show that during the six seconds delay she became restless and often turned around in the release box. In such cases she usually went to boxes *a* or *c*, depending upon the one she *came in line with first* in making a circle by her turning in the release box. It is the writer's opinion that with further training cats can bridge the six seconds delay with three boxes.

(b) *Set B (cats tested on sound).*—

Delay I.—The two cats that continued the work on sound after the death of their fellows were Bess and Phil. Bess was given 60 trials, 48 of which were correct. Of the last 30 trials, 26 or 86% were correct. Phil received 30 trials with 25 or 83% correct, and 9 of the last 10 correct. As in the case of the light experiments, no difficulty was encountered by cutting off the stimulus at this point in the reaction.

Delay II.—One hundred trials were given Bess, and she made 80% correct reactions. Phil received 50 trials which contained 90% correct. Of the last 20 trials 19 were correct. Although the cats were making the last half of the response in the absence of the stimulus, no difficulty yet appeared.

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* Middle box was dropped out here.

Delay III.—On this type of delay, where the stimulus was cut off the moment the cat left the release box, Bess was given 100 trials. Of this number 84 were correct, with 54 of the last 60 correct. Phil made 56 correct reactions out of 70 trials, making a percentage of 80. These results mean that, having started correctly, the cats are able to retain their cue for correct reaction even though the remainder of the reaction must be made in the absence of the stimulus.

Delay IV.—In this delay, Bess was given 60 trials, 55 of which were correct, and, of the last 40 trials, 39 were correct. Phil was given 60 trials with only 60% correct. Of the last 30 presentations, 18 were reacted to correctly. Table V shows Phil's tendency to drop out compartment b whenever the delays set in.

TABLE V

DAILY RECORD ON DELAY 4 WITH SOUND

Cat	Number of trials	Number correct	Distribution of errors		
			a	b	c
Bess	10	10	0	0	0
	10	6	2	2	0
	10	10	0	0	0
	10	9	0	1	0
	10	10	0	0	0
	10	10	0	0	0
			3	3	0
Phil	10	7	0	2	1
	10	7	0	3	0
	10	6	1	2	1
	10	4	0	4	2
	10	7	0	2	1
	10	7	0	3	0
	*10	8	0	2	0
	10	9	0	1	0
	10	8	1	1	0
	10	7	0	3	0
			2	22	5

Two seconds delay.—On this two seconds delay, Bess was given 130 trials and of this number 116 or 89% were correct. Of the last 80 trials, 74 were correct; with the percentage of 92, she was promoted to the four seconds delay. Phil was given

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[*] From January 23rd to February 3rd, Phil was being retrained on delays II and III, receiving 10 trials each day.

60 trials with 51 or 85% correct. Of his last 40 trials, 35 were correct.

Four seconds delay.—One hundred and seventy trials were given Bess with 121 correct responses. Of the last 30, only 18 were correct. With this low record, it was thought best to return to shorter delays before trying to advance. From January 24th, 1916, until February 14th, she was given 10 trials daily on delay IV and on two seconds delays. Of the 200 trials given during this period 120 were given on the two seconds delay, the last 30 of which netted 28 correct reactions. This high percentage of correct reaction on the last 30 is due to the dropping out of the middle box; so, also, may the low percentage of correct reaction immediately preceding be explained by the tendency to drop out the middle boxes the delays were lengthened. The percentage of correct responses in the last 30 trials immediately preceding the dropping out of the middle box was 66, while the percentage of the first 30 after its being dropped out was 94.

(c) *Maximal interval of delay with three boxes.*—

In table VI the maximal delays attained by my cats are given, and for comparative purposes similar data on Hunter's animals and Walton's dogs are included. The reader should remember that these tests were made with a choice of three boxes and that training stopped here because of a well developed tendency to drop out the middle box. In the case of Phil, the last cat reported in the table, this tendency was not well developed. As is shown in the table, he was making a good record on the two seconds delay, and there are no indications that he could not have bridged a longer period of delay with three boxes.

TABLE VI

Animal	Maximal delay	Number of trials	Per cent correct
Hunter........Rats—			
No. 13.............	4 secs.	...	88
No. 15.............	1 sec.	...	86
No. 16.............	1 sec.	...	50
No. 17.............	7 secs.	...	68
Dogs—			
Blackie............	5 mins.	...	80
Brownie...........	2 secs.	...	68

TABLE VI—*Continued*

	Animal	Maximal delay	Number of trials	Per cent correct
	Raccoons—			
	Jill	3 secs.	...	93
	Jack	20 secs.	...	85
	Bob	25 secs.	...	90
Walton	Dogs	10 secs.	...	64
Present work	Cats—			
	Set A (light) Bobby	4 secs.	160	85
	Jim	4 secs.	120	78
	Set B (sound) Bess	4 secs.	170	71
	Phil	2 secs.	40	83

It will be noted that the longest delay mastered by the cats was a period of four seconds. I am sure that with continued training they can bridge a much longer period than this. But, since I was more interested in the behavior during delay than in the maximum period of delay; and since at this point there had developed a tendency to drop out the middle box; and, again, since time was limited, I thought it best not to give further training on three boxes.

(d) *Longer delays.*—

Scattered throughout the experiments are correct reactions over periods of delay much longer than those mastered in the regular series. These periods were willingly lengthened by the subjects themselves. This in itself is good evidence that with sufficient training a much longer interval of delay could be mastered. At three different times Bess made 9 correct reactions out of 10 trials with a delay period of six seconds. And, at another time she made, with the same interval of delay, 17 correct responses out of 20 trials. Twice she responded correctly after a delay period of twenty-six seconds. It will be recalled that Bess was tested on sound. Jim, also tested on sound, bridged at one time a period of eight seconds, at another a period of eighteen seconds, and a third of thirty-four seconds. The cats on light seemed not to have hesitated so often as did those on sound. In all the work on the three box experiments, Bobby was the only cat tested on light who voluntarily lengthened her period of delay. On this occasion she sat for sixty-six seconds in the release box, after which she went directly to the proper compartment. All the periods of hesitation were not measured and tabulated. Animals, both of Set A and Set B, hesitated often from one to three seconds on a single reaction, but their occurrence was so irregular and their duration so brief that their measurement and tabulation were very difficult. Therefore, no period was recorded in seconds unless it was of considerable duration. However, all hesitations were entered in the notes.

2. Two Compartment Experiments

A. "*Delayed*" *experiments.*—The delay work was continued in the two compartment tests by the usual method. The series of presentations of boxes was changed from

ab	cc	ba	ba	cb
bb	ca	ca	bc	ca
ba	ca	bb	ca	ac

One of these three series of ten had been used each night. Each one was used an equal number of times and at no time was one given twice in succession. In this way no one series was given twice within three days. On the two compartment tests the number of series was increased to four, as follows:

ac	ca	ac	ca	ca
ca	ac	ca	ca	ac
aa	ca	ca	ac	ac
cc	aa	ca	ac	ca

These were taken in their order beginning with the first, and no one was, therefore, given twice within four days.

(a) *Cats tested on light.*—It will be remembered that in table IV Jim is reported to have made 29 out of the last 30 trials correct, after a four seconds delay. As his work progresses on the two compartment experiments, the period of delay increases. Since a very large proportion of his errors on the three compartment experiments were due to a tendency to drop out the middle box, he would be expected to make a higher percentage of correct reaction with this box omitted. Such is shown to be the case in the data below.

Of the 40 trials given Jim on six seconds delay 34 were correct. He escaped from the laboratory on the third day, after his work, and after 36 hours absence was recovered and made 80% on 10 trials. Feeling sure that the cat was experiencing no difficulty, the experimenter increased the period of delay to eight seconds. Jim was given 30 trials with this period of delay 27 of which were correct. As he appeared to meet no difficulty in bridging this period, he was set to work on ten seconds delay where he reacted 28 times correctly in 30 trials. On twelve seconds delay he made 90% on 30 trials. Since he had so successfully bridged over these small advances in delays, the next increase was double in length, i.e., four seconds. Forty trials were given with a delay of sixteen seconds. The problem did not seem to increase in difficulty for 36 of these 40 presentations were reacted to correctly.

The longest period of delay in which a regular series of experiments were offered was eighteen seconds. One hundred tests were given Jim on this period of delay, and of this number he responded correctly to 91. During these experiments, Jim was observed as closely as possible as to the orientation of head and body when the door of the release box went up, and also at the moment he initiated the movement of response. The matter of orientation will be taken up again under the discussion of "behavior during delay."

(b) *Cats tested on sound.*—Bess and Phil had been dropped back to the two seconds delay before the middle box was dropped out. Beginning with the two seconds delay they were promoted simultaneously from one interval of delay to another.

Figured on the basis of 30 trials, Bess' percentage jumped from 66 to 95, and Phil's from 80 to 96. On the four seconds delay no difficulty was met. After 40 trials,—Bess with 93% and Phil with 99,—they were promoted to the six seconds delay. Here they received 40 trials, Bess making 95%, while Phil made only 77%. This low percentage on the part of Phil was caused by a pronounced position habit which appeared on the first day and lasted through the second day of the series. They each received 30 trials on both the eight and the ten seconds delays, and each held a percentage of about 85. Since these periods were bridged so easily, the period of delay was now lengthened to fourteen seconds. On this interval of delay, 40 trials were given, and Bess held 87%, while Phil made 98%. Ninety trials were made by each cat on the sixteen seconds delay. Of these 90 trials, Bess was successful 84 times, and Phil 81 times. During this last period of delay of 90 trials, special observation was made of orientation. These observations were recorded in detail, and will be carefully considered under "behavior during delay and after release."

(c) *Maximal interval of delay attained with two boxes.*—Table VII gives the maximal delay attained on two boxes by the subjects studied by Hunter, Walton's dogs, and the cats of the present experiments. The cats rank very well with Hunter's raccoons in successfully bridging delays with two boxes. Just what interval of delay could finally be bridged with the two box tests is not known. It is evident from the above table that the limit of the cats' ability was not reached. I see no reason why the interval may not be increased even into minutes.

TABLE VII

Animal	Maximal delay	Number of trials	Per cent correct
Hunter........Rats—			
No. 4	1 sec.	20	75
No. 11	5 secs.	70	81
No. 15	5 secs.	60	67
No. 16	5 secs.	50	90
Dog—			
Blackie	3 mins.	30	86
Raccoons—			
Jack	20 secs.	40	85
Betty	10 secs.	30	86
Bob	25 secs.	20	90
Walton........Dogs	1 min.	10	80
Present work..Cats—			
Set A—Jim	18 secs.	90	90
Set B—Bess	16 secs.	90	93
Phil	16 secs.	90	90

This opinion is based upon the fact that the records show many reactions where the period of delay is of much longer duration than eighteen seconds, the greatest recorded in the above table. The following long periods of delay were each followed by successful reaction. Phil lengthened his delay period twice during this period of 90 trials, once to twenty seconds and once to twenty-two seconds. Jim reacted correctly after three such periods of delay, twenty-four seconds, twenty-six seconds, and thirty seconds. Bess was successful after the following delays: 1 twenty seconds duration, 3 twenty-two seconds, 1 twenty-four, 1 twenty-six, 1 thirty-two, 2 thirty-six, 1 forty-two, and 1 fifty-two seconds duration.

It will be noted that all animals delayed much longer with two than with three boxes. This is readily explained on the basis of the relative complexity of the problems, and the effect of continued training.

3. Behavior During Delay and After Release

Four different types of behavior appeared in our experiments: (1) The animal maintained an orientation of all its body during the interval of delay, i.e., it kept both its head and body pointing toward the proper box; (2) the animal kept either its head or its body in perfect orientation; (3) no observable part of the animal's body was retained in constant position, i.e., the experimenter could detect no orientation cues used by the animal, (4) the animal held some certain position in the box, i.e., it actually went to the point in the release box nearest to the proper compartment and there awaited to be released. Types 1, 2, and 3 will be combined for convenience in the discussion, and will be followed by a consideration of 4.

A. Orientation of whole or part of body.—Great pains were taken to insure accuracy in the recording of orientations. Records were kept not only of the body position, but of whether *any observable part* of the animal remained in a constant position during the delay period. Also note was made of any case where the animal turned partly or entirely around, as well as of the direction in which it turned. In order to obtain as accurate data as possible on orientation, a series of 300 tests were specially given where the orientations of both the head and body were recorded *at the moment the door of the release box went up, and again when the animal made its first motion to leave the box.* Tables VIII and IX give a summary of these reactions showing just what orientations preceded them. In the first table only those tests are recorded where the orientation was *different* when the animal *started* from what it was when the *door went up.* While in the second table all tests are recorded where the orientation was *the same* when the animal started as it was when the release door went up.

TABLE VIII

When door went up:	Correct	Wrong
Good orientation of head only	108	1
Good orientation of body only	30	1
Good orientation of head and body	118	0
Poor orientation of head and body	18	24

TABLE VIII—*Continued*

When animal started:	Correct	Wrong
Good orientation of head only	2	0
Good orientation of body only	0	1
Good orientation of body and head	259	3
Poor orientation of body and head	9	26

TABLE IX

	Good	Bad
Good orientation lost *between* release and starting	107	1
Good orientation not lost between release and starting	40	0
Poor orientation at release and at starting	4	12

This table indicates plainly the similarity of the behavior of my cats and Hunter's rats and dogs. The cats almost never reacted in opposition to their orientation. (Here I mean, of course, the orientation of both head and body, for many times they reacted correctly in accordance with only the head or the body.) Of 141 errors made by one of Hunter's dogs, 116 were preceeded by faulty orientation. So, also, the cats' errors, as the table shows, were in almost every case preceded by faulty orientation. The non-orientation reactions are few enough to be accounted for by chance.

B. Position in the box.—Owing to the fact that during the period of long delays only two boxes were used and they were located far apart, the cats could have shifted their behavior from the use of *orientation cues* to the use of position cues. Information on this point was hard to get: (1) Because of the continuous movements of the animals, and (2) because the size of the release box in comparison with the distance to the exit box is so small that but little is gained by being at one side or the other. However, from the few observations made, the writer is of the opinion that the position of the animal in the release box does aid its reaction.

4. Reaction Tendencies

In order to get representative data on errors and position habits and the frequency with which these stereotyped forms of response interfered with the work, I shall present 610 of Jim's and 630 of Bess' reactions. It will be remembered that Jim was tested on light and Bess on sound. The first 320 of Jim's 610 reactions were made on the three box experiments, while the remaining 290 were made with only two. Position habits in which one particular box was always chosen first, occurred with each animal on each of the three boxes. Now one box was chosen first and now another. For convenience these data will be recorded in two separate tables (X and XI), the first containing data recorded on the three box experiments, and the second, those obtained when only two boxes were used.

TABLE X

Three Box Experiments

Order of response	abc	acb	ab	ac	Total reactions made
Jim	7	3	22	1	33
Bess	7	1	22	4	34
Order of response	bac	bca	ba	bc	
Jim	0	1	0	1	2
Bess	2	0	7	3	12
Order of response	cab	cba	ca	cb	
Jim	8	6	3	23	40
Bess	0	3	4	15	22

Table X analyzes all incorrect responses made on the three box experiments, here included, and gives the relative number of times each subject followed the different possible orders. The number of errors made beginning with boxes *a* and *c* is about equal with both animals, while the number beginning with *b* is very low. In fact, as the table shows, Jim only made 2 errors when *b* was selected first. Bess, however, made 12 such errors, or about one-half the number she made after selecting *c* first. Of the 40 times Jim selected *c* first, he selected *b* next 29, or 72% of the time. And of the 33 times he selected *a* first, 29, or 87% of the time *b* was the next box selected. When *a* was selected first by Bess, she chose *b* next 29 times out of 34, or 85% of the time. And when she selected *c* first, she chose *b* next 18 times out of 22, or 81% of the time. It may be concluded then, that whenever the reaction began at the end of the row of boxes, i.e., *a* or *c*, the tendency was to take the boxes in order until the solution was reached. Only three times in 320 trials did Jim go to the same box twice in the same trial. (These are listed in table XII as "persistent errors.") The form of this position habit was c b c b a, and was repeated three times within 20 trials. Bess returned to the same box in the same trial only one time, and the order of the boxes chosen was b a b c. One further thing to be noted is that Jim made 25 "three place errors," responses where the animal tests each of the three boxes before the solution is reached. This type of error was made 13 times by Bess. This form of behavior is apparently less frequent than in Hunter's child[3] and far less frequent than in Hamilton's dog.[4]

TABLE XI

TWO BOX EXPERIMENTS*

Order of response	abc	ac	bac	ba	Total reactions made
Jim	0	14	0	0	14
Bess	6	14	0	0	20
Order of response	bca	bc	cba	ca	
Jim	0	0	0	15	15
Bess	0	0	0	6	6

* Since exit *b* is no longer open, all orders of choice ending in *b* are omitted in this table.

Table XI contains a record of the errors made in the two box experiments. Jim had so completely lost the cue to *b* that not one time after that box was dropped out did he return to it. Although Bess never made *b* her first choice again, she at six different times on her way from *a* over to *c* stopped by and examined *b*. It will be noticed that the number of errors greatly decreased with the elimination of the middle box. This may be accounted for, first, by the increase in the simplicity of the problem and, second, by practice.

It would be well worth while to put beside the reaction tendencies of these two cats similar data gathered by Hunter on rats, raccoons, dogs, and children. Table XII gives a summary of the errors made by his subjects, and includes, also, those for my two cats. Some explanation of this table is necessary.

TABLE XII

Animal	Number of trials	Total number of errors A	Three place errors B	Persistent errors C	Per cent of A to B	Per cent of B to C
Child	264	120	54	6	44	11
Raccoon—Bob	720	209	78	29	32	37
Dog—Blackie	570	127	75	25	59	33
Rat—No. 9	575	144	42	13	29	30
No. 2	345	152	69	47	45	68
Cat—Jim	320	75	25	3	33	12
Bess	330	68	13	1	19	7

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[3] Hunter, W. S. The delayed reaction in a child. *Psych. Rev.*, 1917, vol. 24, 74-87.

[4] Hamilton, G. V. T. An experimental study of an unusual type of reaction in a dog. *Jour. Comp. Neur. Psy.*, 1907, **17**, 329-341.

The raccoon's records include delays from one second through twenty seconds; those for the dog, from one second through seven seconds; those for rat No. 9, from the third stage of delay (turning light off just as the animal was released) through seven seconds; those for rat No. 2, from the third stage of the delay through one second; and those for Jim and Bess, from one second through four seconds. The data are compiled here for comparative purposes and will be easily interpreted without further comment.

Available data at the time of the preparation of Hunter's paper on the delayed reaction in a child made it clear that there were no marked differences between animals in the reaction tendencies displayed under the experimental conditions in question. It did look, however, as though there were marked differences between the animals and the child. Our data here presented place the cats in a class with the child. So far then as this type of test is concerned, no essential differences between man and other animals have been brought to light.

CONCLUSIONS

1. All the cats herein tested learned the initial association within from 100 to 180 trials and therefore fall into a class with Hunter's raccoons, so far as rapidity of learning is concerned.
2. No differences of method in solution of delays was observed between cats on light and those on sound.
3. The minimum and maximum delays were two seconds and four seconds on the three compartment experiments; while with only two compartments, they increased to sixteen seconds and eighteen seconds respectively.
4. The cats solved the problem by maintaining gross motor attitudes of the whole or part of the body.

TEMPERAMENTAL DIFFERENCES BETWEEN OUTBRED AND INBRED STRAINS OF THE ALBINO RAT

NENOZO UTSURIKAWA

From the Harvard Psychological Laboratory

INTRODUCTION

About two years ago the writer sought, in the Harvard Psychological Laboratory, training in the methods of comparative psychology, since such training promised to be helpful to him as an ethnologist. A problem was suggested to him by Professor R. M. Yerkes,—evidently difficult and yet extremely fascinating. Its thorough study would certainly require years of diligent work. But the writer, because of his ethnological interests, was able to give only one year to this psychological investigation.

Obviously enough, from what follows, the materials to be presented are fragmentary and inadequate for the description of the differences in the strains of rat. Still, to throw them away would seem too extravagant. With a humble sense of obligation, the writer offers his limited data to the scientific world. He wishes to take this opportunity to thank Professor Yerkes, Dr. R. M. Elliott, and Dr. W. R. Miles, for valuable assistance in the work.

PROBLEMS

The chief problem was to discover, if any, the temperamental differences between outbred and inbred strains of the albino rat. Such features of behavior as degree of nervousness or timidity, of savageness and wildness, of sensitiveness to stimuli, of persistence in response, quickness of response, and so on, may be recorded as constituting the temperament of an animal. In the terms of psychology, and in the last analysis, perhaps, temperament is identical with the threshhold, quickness, amount, and steadiness of response to a given stimulus or object. The problem, therefore, requires the measurement of the essential components of temperament in order that comparisons of the two strains may be made.

Although the inquiry was directed mainly to temperamental characteristics, differences in behavior of other sorts were noted and may here be reported. From the anthropologist's point of view, the study of close inbreeding and its consequences, even in case of lower animals, is of extreme interest and of some practical importance. Anthropological data concerning this matter are meager, and as Topinard remarks, " the question is still *sub judice*." Possibly it is not far from the truth to say that such information concerning man will long be lacking, whereas, through the study of infra-human organisms, we can readily approach reliable information. Infra-human psychology gains in importance as it allies itself with human psychology, and this paper, if not projected upon the background of larger human interests, will lose much of its significance.

There is such meager literature on temperamental characteristics of lower animals that a historical summary is unnecessary. The contribution of Basset[1] to the study of albino rats alone has fairly direct bearing upon the materials of this paper.

SUBJECTS

Only albino rats were observed. All were obtained either from the Wistar Institute of Anatomy and Biology in Philadelphia or from Miss A. E. C. Lathrop, Granby, Mass. The several inbred rats were from the inbred strain of the Wistar Institute. We are greatly indebted for them to Dr. H. H. Donaldson and Dr. H. D. King. The accompanying list supplies the reader with all available data concerning individuals on whom the observations of this report were made.

Outbred Stock

Number of rat	Source and parentage	Date of birth	Experiment begun
251 ♂	Granby*	August 5, 1914	October 14, 1914
252 ♀	"	"	"
253 ♂	"	"	"
254 ♀	"	"	"

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[1] Basset, G. C. Habit formation in a strain of albino rats of less than normal brain weight. *Behavior Monographs*, 1914, **2**, no. 4.

OUTBRED STOCK—*Continued*

Number of rat	Source and parentage	Date of birth	Experiment begun
1 ♂	Wistar	September —, 1914	November 5, 1914
2 ♀	“	“	“
3 ♂	“	“	“
4 ♀	“	“	“
261 ♂	Granby, 251 ♂ x 252 ♀	October 28, 1914.	March 2, 1915
262 ♀	“ “	“	“
263 ♂	“ “	November 28, 1914	“
264 ♀	Wistar, 3♂ x 4♀	November 25, 1914	“
265 ♂	“ “	“	“
266 ♀	Granby, 251 ♂ x 252 ♀	November 28, 1914	“

* Purchased of Abbie E. C. Lathrop, Granby, Mass.

INBRED STOCK

Number of rat	Source and generation of inbreeding	Date of birth	Experiment begun
201 ♂	Wistar, 14th	August 8, 1914	October 14, 1914
202 ♀	“	“	“
203 ♂	“	“	“
204 ♀	“	“	“
5 ♂	“	September —, 1914	November 5, 1914
6 ♀	“	“	“
7 ♂	“	“	“
8 ♀	“	“	“
211 ♂*	Wistar, 15th	December 18, 1914	April 11, 1915
212 ♀*	“	“	“
213 ♂*	“	“	“
214 ♀*	“	“	“
215 ♂*	“	“	“
216 ♀*	“	“	“

* Offspring of 201 ♂ x 202 ♀.

METHOD OF INQUIRY

Observations were made for above strains of rat as nearly as possible at the same age, and for the sake of comparability, on the same day. Certain of the observations were made under the natural cage conditions; others, under definite experimental conditions and for very specific purposes. These two kinds of data, contrasted as the naturalistic and the experimental, tend to supplement one another.

The naturalistic type of observation includes (1) observation of the position of an individual in the cage or nest box; (2) of the relative positions of the two individuals, male and female, in the cage; (3) of the degree of activity in the cage; (4) of savageness, viciousness, or tendency to bite. The experimental observation includes (1) measurements of quickness of response to auditory stimuli; (2) of amount of movement in response to the same stimuli; (3) of general behavior (restlessness) during stimulation.

These several varieties of observation will now be reported in tabular form, with scant discussion.

POSITION OF RAT IN CAGE

The animals were kept in rectangular, all-wire cages, the floor dimensions of which were 16 inches by 14 inches. A single pair of individuals, either outbred or inbred, was kept in a cage. When the writer came into the animal room to feed the rats, many of them would, as a rule, come forward in expectation of food, but some would remain at the back of the cage or retreat to the distant portion of the cage as the experimenter approached. Some came forward singly; others, together. Sometimes the individuals were found lying together in the cage; at other times they were observed to be distant from one another. The data of table 1 concern, first, position of the two animals, male and female, in the cage when the experimenter entered the room; and second, the positions of male and female with relation to one another.

TABLE 1

POSITION OF RATS IN CAGE

OUTBRED RATS

Date	Number of rat	Position forward	Male and female together
Oct. 15 on	251 ♂	$\frac{77}{110} = .70$	$\frac{9}{110} = .08$
“	253 “	$\frac{76}{100} = .76$	$\frac{7}{100} = .07$
Mar. 2 on	261 “	$\frac{40}{60} = .67$	$\frac{12}{60} = .20$
“	263 “	$\frac{41}{60} = .68$	$\frac{18}{60} = .30$

TABLE 1—*Continued*

Date	Number of rat	Position forward	Male and female together
“	265 ♂	$\frac{57}{60} = .95$	$\frac{27}{60} = .45$
Nov. 5 on	1 “	$\frac{65}{90} = .72$	$\frac{9}{90} = .10$
“	3 “	$\frac{43}{80} = .54$	$\frac{23}{80} = .29$
Average		$\frac{437}{700} = .62$	$\frac{98}{700} = .14$
Oct. 15 on	252 ♀	$\frac{82}{110} = .75$	$\frac{9}{110} = .08$
“	254 “	$\frac{71}{100} = .71$	$\frac{7}{100} = .07$
Mar. 2 on	262 “	$\frac{47}{60} = .78$	$\frac{12}{60} = .20$
“	264 “	$\frac{10}{60} = .17$	$\frac{18}{60} = .30$
“	266 “	$\frac{57}{60} = .95$	$\frac{27}{60} = .45$
Nov. 5 on	2 “	$\frac{76}{90} = .84$	$\frac{9}{90} = .10$
“	4 “	$\frac{65}{90} = .72$	$\frac{23}{80} = .29$
Average		$\frac{490}{700} = .70$	$\frac{98}{700} = .14$

Position of Rats in Cage

Inbred Rats

Date	Number of rat	Position forward	Male and female together
Oct. 15 on	201 ♂	$\frac{40}{110} = .36$	$\frac{43}{110} = .39$
“	203 “	$\frac{40}{120} = .33$	$\frac{24}{50} = .48$
Mar. 2 on	211 “	$\frac{26}{30} = .87$	$\frac{11}{30} = .37$

TABLE 1—*Continued*

INBRED RATS—*Continued*

Date	Number of rat	Position forward	Male and female together
Mar. 2 on	213 ♂	$\frac{30}{30}=1.00$	$\frac{19}{30}=.63$
“	215 “	$\frac{27}{30}=.90$	$\frac{12}{30}=.40$
Nov. 5 on	5 “	$\frac{28}{80}=.35$	$\frac{41}{80}=.51$
“	7 “	$\frac{63}{90}=.70$	$\frac{22}{90}=.24$
Average		$\frac{306}{700}=.44$	$\frac{293}{700}=.42$
Oct. 15 on	202 ♀	$\frac{39}{110}=.35$	$\frac{43}{110}=.39$
“	204 “	$\frac{26}{50}=.52$	$\frac{24}{50}=.48$
Mar. 2 on	212 “	$\frac{26}{30}=.87$	$\frac{11}{30}=.37$
“	214 “	$\frac{29}{30}=.97$	$\frac{19}{30}=.63$
“	216 “	$\frac{27}{30}=.90$	$\frac{12}{30}=.40$
Nov. 5 on	6 “	$\frac{31}{90}=.34$	$\frac{49}{90}=.54$
“	8 “	$\frac{58}{90}=.64$	$\frac{22}{90}=.24$
Average		$\frac{329}{700}=.47$	$\frac{293}{700}=.42$

The fractions of column 3 in this table indicate the relative frequency of the forward position, that is, the presence of a rat forward or its movement to that position on the approach of the experimenter. The numerator of the fraction indicates frequency of this position; the denominator indicates the total number of observations on the individual.

The chief results of these observations on the position of the animals in the cage and their relation to one another may be stated thus:

(1) Outbred individuals more frequently come forward in the cage than inbred.

(2) Females more frequently come forward than males.

(3) Individual differences are greater than are the differences between the two strains or the two sexes.

(4) Inbred males and females are found together 3 times as frequently as are outbred males and females.

ACTIVITY

The degree of activity of the several rats, as indicated by their walking, running, climbing, washing, sniffing, seeking for food, lifting the lid of the cage, and so on, was observed and roughly graded by means of the numerals 0 to 5, 0 indicating minimum activity and 5 maximum activity.

As in the previous case, tabular presentation is possible, and in table 2 appear the comparable data for the two strains. In this table, the numerator of the fraction is the sum of the various grades given an animal in the total number of observations, which appears as the denominator of the fraction. The average grade in decimals in each case follows the fraction.

TABLE 2

AMOUNT OF ACTIVITY OF RATS

Outbred			Inbred		
Date	No. of rat	Activity	Date	No. of rat	Activity
Oct. 15 on	251 ♂	$\frac{286}{110} = 2.6$	Oct. 15 on	201 ♂	$\frac{163}{110} = 1.5$
“	253 “	$\frac{221}{100} = 2.2$	“	203 “	$\frac{103}{120} = .9$
Mar. 2 on	261 “	$\frac{145}{60} = 2.4$	Mar. 2 on	211 “	$\frac{66}{30} = 2.2$
“	263 “	$\frac{103}{60} = 1.7$	“	213 “	$\frac{59}{30} = 2.0$
“	265 “	$\frac{94}{60} = 1.6$	“	215 “	$\frac{70}{30} = 2.3$

TABLE 2—*Continued*

Outbred			Inbred		
Date	No. of rat	Activity	Date	No. of rat	Activity
Nov. 5 on	1 ♂	$\frac{191}{90} = 2.1$	Nov. 5 on	5 ♂	$\frac{116}{80} = 1.5$
“	3 “	$\frac{101}{80} = 1.3$	“	7 “	$\frac{174}{90} = 1.9$
Average		$\frac{139}{70} = 2.0$	Average		$\frac{123}{70} = 1.8$
Maximum		2.6	Maximum		2.3
Minimum		1.3	Minimum		.9
Oct. 15 on	252 ♀	$\frac{266}{110} = 2.4$	Oct. 15 on	202 ♀	$\frac{174}{110} = 1.6$
“	254 “	$\frac{248}{100} = 2.5$	“	204 “	$\frac{51}{50} = 1.0$
Mar. 2 on	262 “	$\frac{147}{60} = 2.5$	Mar. 2 on	212 “	$\frac{68}{30} = 2.3$
“	264 “	$\frac{67}{60} = 1.1$	“	214 “	$\frac{54}{30} = 1.8$
“	266 “	$\frac{130}{60} = 2.2$	“	216 “	$\frac{62}{30} = 2.1$
Nov. 5 on	2 “	$\frac{213}{90} = 2.4$	Nov. 5 on	6 “	$\frac{120}{90} = 1.3$
“	4 “	$\frac{202}{90} = 2.2$	“	8 “	$\frac{143}{90} = 1.6$
Average		$\frac{152}{70} = 2.2$	Average		$\frac{117}{70} = 1.7$
Maximum		2.5	Maximum		2.3
Minimum		1.1	Minimum		1.0

Three comparative statements are justified by the data of table 2:

(1) Outbred rats are more active than inbred.

(2) The activity of the sexes differs much more for the outbred strain than for the inbred.

(3) Individual differences in activity are greater than either sex or strain differences.

SAVAGENESS OR VICIOUSNESS AS INDICATED BY THE TENDENCY TO BITE

As a means of testing the savageness of the rats, a copper wire was thrust into the cage from the front and from above, and the floor was scraped or scratched with it. Some individuals would, at this, dash forward and bite viciously and persistently at the wire, whereas others merely noticed the disturbance and were otherwise indifferent to it. The method of grading this behavior was similar to that used in the case of activity.

The essential statistical data from these observations appear as table 3.

TABLE 3

SAVAGENESS OR VICIOUSNESS (BITING) OF RATS

Outbred			Inbred		
Date	No. of rat	Savageness (biting)	Date	No. of rat	Savageness (biting)
Oct. 15 on	251 ♂	$\frac{92}{110} = .84$	Oct. 15 on	201 ♂	$\frac{31}{110} = .28$
"	253 "	$\frac{4}{100} = .04$	"	203 "	$\frac{109}{120} = .91$
Mar. 2 on	261 "	$\frac{2}{60} = .03$	Mar. 2 on	211 "	$\frac{79}{30} = 2.63$
"	263 "	$\frac{1}{60} = .02$	"	213 "	$\frac{74}{30} = 2.47$
"	265 "	$\frac{48}{60} = .80$	"	215 "	$\frac{26}{30} = .87$
Nov. 5 on	1 "	$\frac{10}{90} = .11$	Nov. 5 on	5 "	$\frac{6}{80} = .08$
"	3 "	$\frac{34}{80} = .43$	"	7 "	$\frac{35}{90} = .39$
Average		$\frac{226}{700} = .32$	Average		$\frac{763}{700} = 1.09$
Maximum		.84	Maximum		2.63
Minimum		.02	Minimum		.08
Oct. 15 on	252 ♀	$\frac{6}{110} = .05$	Oct. 15 on	202 ♀	$\frac{86}{110} = .78$
"	254 "	$\frac{52}{100} = .52$	"	204 "	$\frac{161}{50} = 3.22$

TABLE 3—*Continued*

Outbred			Inbred		
Date	No. of rat	Savageness (biting)	Date	No. of rat	Savageness (biting)
Mar. 2 on	262 ♀	$\frac{224}{60} = 3.73$	Mar. 2 on	212 ♀	$\frac{83}{30} = 2.77$
“	264 “	$\frac{99}{60} = 1.65$	“	214 “	$\frac{22}{30} = .73$
“	266 “	$\frac{60}{60} = 1.00$	“	216 “	$\frac{87}{30} = 2.90$
Nov. 5 on	2 “	$\frac{209}{90} = 2.32$	Nov. 5 on	6 “	$\frac{163}{90} = 1.81$
“	4 “	$\frac{301}{90} = 3.34$	“	8 “	$\frac{440}{90} = 4.89$
Average		$\frac{1261}{700} = 1.80$	Average		$\frac{1710}{700} = 2.44$
Maximum		3.73	Maximum		4.89
Minimum		.05	Minimum		.73

The females far exceeded the males in degree of savageness. They were, moreover, surprisingly quick and aggressive, whereas the males were either on the defensive or indifferent. Whether this remarkable sex difference is correlated with the maternal instinct is not clear. It is, however, noteworthy that in the feeding behavior the male very obviously asserts himself and becomes the aggressor. It further appears from these observations that the tendency to bite is not directly proportional to activity. Instead, there seems to be a tendency toward an inverse relation.

The chief facts concerning savageness in the two strains are these:

(1) Females are much more savage (exhibit the tendency to bite more often and persistently) than are males.

(2) The inbred rats are much more savage than the outbred.

(3) Individual differences exceed either sex or strain differences, and they are especially great in case of the females.

EXPERIMENTAL OBSERVATIONS

The writer had intended to record the responses of his animals to various stimuli and to more complex situations by means of the galvanometer. But as the resources of the laboratory at the time did not permit of the development of a suitable form of apparatus, this plan was abandoned in favor of a less expensive and cruder preliminary mode of observation.

The apparatus finally devised and used consisted of a small blackened rectangular box which rested at one end on two pointed metallic posts and was suspended at the other end by a delicate spring. This box was connected with a kymograph by means of a marking lever so that any vertical movement of the box was recorded on the kymograph surface. The rat was placed in the box and so confined by means of movable partitions that it was forced to hold its orientation with head pointed forward toward the writing lever. The front end of the box consisted of a wire screen. On the kymograph three records were written: (1) A time line, indicating fifths of a second; (2) a stimulus line; (3) a response line.

The only mode of stimulation here reported is the auditory, and for this purpose an electric bell was used.

The reaction box and stimulus apparatus were enclosed in a large pasteboard box in order that the animal should be somewhat protected from disturbing conditions.

QUICKNESS OF RESPONSE TO AUDITORY STIMULI

A rat having been placed in the apparatus and allowed to become accustomed to its position, the various parts of the mechanism were carefully adjusted, and when everything was in readiness an auditory stimulus was given for .5 to .6 of a second. After eight seconds, the stimulus was repeated. Then the experimenter waited for an interval of another eight seconds before again presenting a pair of auditory stimuli.

The quickness of response was indicated by the distance between the point of stimulation on the stimulus line and the point of initial response on the reaction line. The measurement is extremely crude and inaccurate, but so far as may be judged, not more so for the one strain or the one sex than for the other. Where, because of long delayed or indefinite response, it was difficult to decide on the initial point, the reaction was ignored.

The data of table 4 include the mean or average reaction time for each individual in the first trial, that is, after initial stimulus, and in the second trial, that is, with repetition of the stimulus, the maximal and minimal reaction times, the total number of trials, and the number of trials in which no response appeared. The chief results of these measurements of reaction time may be stated thus:

TABLE 4

Quickness of Response to Auditory Stimulus

Outbred

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
251 ♂	.35″*	.8″*	0*	3	10	.98″*	1.8″*	0	5	10
261 "	.39″	.9″	0	8	17	.21″	.35″	0	12	17
263 "	.51″	1″	0	3	16	.30″	1.2″	0	5	16
265 "	.51″	1″	0	7	15	.46″	1.2″	0	9	15
	Aver. .47″	1″	0	Total 21	Total 58	Aver. .32″	1.2″	0	Total 31	Total 58

Average reaction time for the first and second trials........... = .40″
Total number of failures to respond in the first and second trials = 52

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
252 ♀	.43″*	1.0″*	0	3	10	.63″*	1.8″*	0	1	10
262 "	.38″	.7″	0	4	17	.43″	.95″	0	7	17
264 "	.15″	.3″	0	5	17	.30″	.7″	0	4	17
266 "	.28″	.6″	0	6	14	.80″	.8″	0	9	14
	Aver. .27″	.7″	0	Total 18	Total 58	Aver. .51″	.95″	0	Total 21	Total 58

Average reaction time for the first and second trials........... = .39″
Total number of failures to respond in the first and second trials = 39

* Excluded from the averages, as the accuracy of measurements was uncertain.

INBRED

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
201 ♂	.42″*	.7″*	.08″*	0	10	.33″*	.7″*	0*	1	10
211 "	.18″	.3″	0	3	16	.26″	1.2″	0	3	16
213 "	.19″	.3″	0	1	16	.14″	.3″	0	9	16
215 "	.17″	.4″	0	2	16	.13″	.2″	0	7	16
	Aver. .18″	.4″	0	Total 6	Total 58	Aver. .18″	1.2″	0	Total 20	Total 58

Average reaction time for the first and second trials........... = .18″
Total number of failures to respond in the first and second trials = 26

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
202 ♀	.26″*	2.0″*	.01″*	1	10	.30″*	.6″*	0	3	10
212 "	.23″	.85″	0	3	16	.22″	.65″	0	4	16
214 "	.29″	.5″	0	8	16	.08″	.08″	0	13	16
216 "	.28″	.8″	0	6	16	.23″	.8″	0	5	16
	Aver. .27″	.85″	0	Total 18	Total 58	Aver. .18″	.8″	0	Total 25	Total 58

Average reaction time for the first and second trials........... = .23″
Total number of failures to respond in the first and second trials = 43

* Excluded from the averages as the accuracy of measurements was uncertain.

(1) Inbred rats respond more quickly to the auditory stimulation than do outbred. (a) Inbred males respond most quickly of all (.18 seconds). (b) Inbred females rank next in quickness of response (.23 seconds). (c) Outbred females rank third (.39 seconds). (d) Outbred males are slowest of all (.40 seconds).

(2) The number of failures to respond obviously to the auditory stimulation is both smallest and greatest for the males. (a) The inbred males failed to respond 26 times in 116 trials. (b) The outbred females failed to respond 39 times in 116 trials.

(c) The inbred females failed to respond 43 times in 116 trials.
(d) The outbred males failed to respond 52 times in 116 trials.

(3) The reaction time of the males is extremely variable; that of the females is comparatively uniform.

(4) The sex difference in reaction time for inbred rats is slightly more than for outbred.

(5) Reaction time, with certain exceptions, is shorter in case of the second trial (repetition of auditory stimulus) than in the first. Failures to respond are more frequent in the second trial than in the first.

(6) Individual differences exceed sex and strain differences.

AMOUNT OF RESPONSE TO AUDITORY STIMULI

The amount of motor response to auditory stimuli was determined by multiplying the maximum length (straight line) of the response curve by the maximum height (straight line). The result is expressed in square centimeters. These measurements are even less reliable than those of reaction time, but again there seems no reason to suppose that the errors are unequal for either the sexes or the strains of rat.

As previously, the statistical data are arranged in tabular form. They appear in table 5.

TABLE 5

Amount of Response to Auditory Stimuli

Outbred

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
251 ♂	16.3	64	0	3	10	15.2	32	0	5	10
261 "	3.1	20	0	10	17	1.1	10	0	14	17
263 "	8.9	40	0	6	16	2.6	40	0	10	16
265 "	6.0	20	0	8	14	6.4	40	0	9	14
	Aver. 8.6	64	0	Total 27	Total 57	Aver. 6.3	40	0	Total 38	Total 57

Average amount of response for the first and second trials..... = 7.5 c.c.
Total number of failures to respond in the first and second trials = 65

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
252 ♀	65.6	280	0	3	10	39.7	168	0	1	10
262 “	24.0	120	0	5	17	11.5	88	0	9	17
264 “	7.9	48	0	5	16	6.0	20	0	4	16
266 “	15.4	48	0	5	13	1.4	14	0	9	13
	Aver. 28.2	280	0	Total 18	Total 56	Aver. 14.7	168	0	Total 23	Total 56

Average amount of response for the first and second trials..... = 21.5 c.c.
Total number of failures to respond in the first and second trials = 41

INBRED

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
201 ♂	18.1	36	2	0	16	11.3	72	0	1	16
211 “	13.9	50	0	3	16	2.9	12	0	5	16
213 “	24.1	120	0	4	16	7.0	40	0	10	16
215 “	27.9	180	0	3	16	8.2	80	0	8	16
	Aver. 21.0	180	0	Total 10	Total 64	Aver. 7.4	80	0	Total 24	Total 64

Average amount of response for the first and second trials..... = 14.2 c.c.
Total number of failures to respond in the first and second trials = 34

Number of rat	First trial					Second trial				
	Mean	Max.	Min.	No resp.	No. of trials	Mean	Max.	Min.	No resp.	No. of trials
202 ♀	133.1	640	0	1	16	35.3	192	0	3	16
212 "	29.0	96	0	4	16	17.1	168	0	7	16
214 "	14.4	48	0	8	16	11.3	144	0	12	16
216 "	9.5	44	0	6	16	8.0	48	0	10	16
	Aver. 46.5	640	0	Total 19	Total 64	Aver. 17.9	192	0	Total 32	Total 64

Average amount of response for the first and second trials..... = 32.2
Total number of failures to respond in the first and second trials = 51

The following conclusions are indicated by the measurements of amount of response:

(1) The response of outbred rats is far less than that of inbred.

(2) The response of females is greater than that of males.

(3) The response is less in the second trial than in the first.

(4) Individual and sex differences in amount of response far exceed strain differences.

GENERAL BEHAVIOR DURING AUDITORY STIMULATION

As an indication of the restlessness or general tendency to activity as a result of auditory stimulation, the total length of the response curve was measured by means of a chartometer. This could be done only very inaccurately because of the many slight changes in direction of the curve, but as in the case of previous experiments, there is no reason to suppose that the degree of accuracy varies with the strains or with the sexes.

Measurements of restlessness were made for two conditions of stimulation: (a) For separate auditory stimuli, the one following the other after a stated interval and thus giving in the records trial 1 and trial 2; and (b) for continuous auditory stimulation instead of momentary.

Table 6 presents the data of restlessness or general behavior. The principal results may be summarily stated thus:

TABLE 6

BEHAVIOR DURING EXPERIMENT

OUTBRED

Number of rat	With intermittent stimulation				With continuous stimulation			
	Mean	Max.	Min.	No. of trials	Mean	Max.	Min.	No. of trials
251 ♂	17.4*	19.0	17.0	10	18.1	20.0	17.1	3
261 “	17.2	17.5	17.0	18	17.2	18.5	17.0	18
263 “	17.3	19.0	17.0	17	17.2	17.8	17.0	17
265 “	17.6	21.8	17.0	15	17.3	18.0	17.0	15
	Average 17.4	21.8	17.0	Total 60	Average 17.5	20.0	17.0	Total 53

Average of both responses to intermittent and continuous stimulations = 17.5

Number of rat	With intermittent stimulation				With continuous stimulation			
	Mean	Max.	Min.	No. of trials	Mean	Max.	Min.	No. of trials
252 ♀	22.5	38.2	17.0	10	23.3	26.2	20.5	2
262 “	17.4	18.0	17.0	18	19.5	38.5	17.0	18
264 “	18.4	22.7	17.0	17	18.4	21.0	17.0	17
266 “	17.3	18.5	17.0	14	18.1	21.0	17.0	14
	Average 18.9	38.2	17.0	Total 59	Average 19.8	38.5	17.0	Total 51

Average of both responses to intermittent and continuous stimulations = 19.4

* Expressed in centimeters.

INBRED

Number of rat	With intermittent stimulation				With continuous stimulation			
	Mean	Max.	Min.	No. of trials	Mean	Max.	Min.	No. of trials
201 ♂	17.7	20.0	17.0	10	17.5	18.0	17.0	5
211 "	17.8	24.0	17.0	16	18.9	21.6	17.1	16
213 "	17.2	17.5	17.0	16	17.6	21.0	17.0	16
215 "	19.2	18.2	17.0	16	17.4	20.0	17.0	16
	Average 18.0	24.0	17.0	Total 58	Average 17.9	21.6	17.0	Total 53

Average of both responses to intermittent and continuous stimulations = 18.0

Number of rat	With intermittent stimulation				With continuous stimulation			
	Mean	Max.	Min.	No. of trials	Mean	Max.	Min.	No. of trials
202 ♀	20.1	30.5	17.0	11	17.3	17.5	17.1	5
212 "	17.7	23.0	17.0	16	17.8	22.0	17.0	16
214 "	18.2	21.5	17.0	16	18.7	26.0	17.0	16
216 "	17.6	24.5	17.0	16	17.6	24.0	17.0	16
	Average 18.4	30.5	17.0	Total 59	Average 17.9	26.0	17.0	Total 53

Average of both responses to intermittent and continuous stimulations = 18.2

(1) For inbred rats, the restlessness or continuity of response is greater in case of momentary and repeated auditory stimulation, whereas for outbred rats, the reverse is true.

(2) The amount of restlessness varies more widely for outbred than for inbred rats.

(3) The females of both strains show higher records for restlessness than do the males.

(4) The records for the females are also more variable than for the males, with averages as follows: Outbred males, 17.5;

inbred males, average 18.0; outbred females, average 19.4; inbred females, average 18.2.

(5) Individual and sex differences greatly exceed strain differences.

CONCLUSIONS

The outbred and inbred strains of albino rats contrast in temperament as follows:

(1) Inbred males and females are found together in the cage about three times as frequently as are outbred.

(2) The inbred rats come forward in the cage on the approach of the experimenter much less frequently than do the outbred.

(3) Inbred rats are less active than outbred.

(4) The inbred stock exhibits savageness by biting to approximately twice the extent of the outbred.

(5) The inbred animals respond more quickly and in greater amount to momentary auditory stimulation than the outbred.

(6) The two strains differ also in restlessness or continuity of response. For the inbred restlessness is greatest in case of momentary and repeated auditory stimulation and less in case of continuous stimulation, whereas for the outbred animals, the reverse is true.

(7) The data indicate less difference between the sexes in the inbred than the outbred rats.

RETROACTIVE ASSOCIATION AND THE ELIMINATION OF ERRORS IN THE MAZE

HELEN B. HUBBERT AND K. S. LASHLEY

The temporal relation of the different activities which are associated in the formation of a habit seems to have a direct bearing upon the form in which the habit is fixed. Thus in an experiment described by Bohn (Dontchef-Dezeuze, '14), carried out in Pawlow's laboratory, the selection of stimulus and response by their temporal relation seems established. In this experiment an electrical stimulus was applied to the skin of a dog, eliciting struggling and howling. Following this, food was placed in the animal's mouth and salivary secretion was obtained as a result. After this sequence had been repeated many times the only reaction to the electrical stimulation of the skin was the secretion of saliva. Why, in this experiment, was the secretion of the saliva associated with the electrical stimulus and not the struggling and howling with the taste of food? An animal may be trained readily to reject food with the latter reactions in a given situation by the use of punishment after food is taken,[1] so it seems that the temporal order determined which of the stimuli and responses were to become associated.

In the formation of complex habits it is probable that similar and even more complex temporal factors modify the course of learning. Hachet-Souplet ('13) has stated dogmatically that when a series of actions, leading up to a pleasurable situation, becomes connected into a habit the association occurs first between the activities just preceding the pleasant result and progresses to those more remotely antecedent. This may be called the principle of retroactive association. If it is a fact it has an important bearing upon theories of the mechanism of selection in habit-formation.

In the work with the conditioned reflex it has been shown that a well established reflex may serve as a basis for the formation of other conditioned reflexes as well as can an unconditioned reflex (Bechterew, '13). If this condition obtains in the formation of a maze-habit, the situation involved in the last turn before the food is reached may acquire from the getting of food something (we can not be more definite at present) which makes it capable of serving instead of the food in the fixation of the next preceding activity. In this case the formation of a maze-habit would appear as a series of secondary, tertiary, etc., conditioned reflexes starting from the taking of food as the primary reflex and progressing from the food compartment outward to the entrance of the maze. Such an explanation avoids one of the chief difficulties of theories of the fixation of habit; that of accounting for the effects of getting food, or what not, upon an activity which occurred half an hour or more earlier, such as turning in a given direction at the entrance to the maze.[2]

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[1] Hachet-Souplet ('14) describes an interesting case of this sort.

But such an hypothesis must be looked upon with suspicion until the fact of retroactive association is established, and there is little evidence in favor of this at present. With a slightly different problem in view Hubbert ('15) has made an analysis of the order of elimination of errors in the maze. The results of this analysis were not very certain owing to confliction in the data given by different groups of animals. One point was quite clear, however; there is no invariable sequence in the elimination of errors, if the records of single animals are considered. In contrast to this, when the averages of very large groups of animals are taken there does seem to be a progressive elimination of errors from the food compartment to the entrance of the maze. This is shown by the following averages based upon all the data given by Hubbert. (See figure 1 for the designation of the alleys.)

a	b	c	d	e	f	
30.6	26.4	19.7	19.7	18.7	8.3	trials.

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[2] The theories of nervous drainage such as those formulated by Pawlow, Max Meyer, Watson, and others seem to require the immediate succession of the acts associated. In the experiments of Bohn, for example, they must assume that the salivary reflex is excited while the nervous elements of the struggling reflexes are still active and that the efferent fibres of the salivary glands drain off a part of the energy from the cutaneous stimulation, thus opening the synapses from the receptors of the skin to the salivary glands. None of the other theories of the physiology of learning has been formulated in sufficient detail to take into consideration the possibility of retroactive association.

In the individual records we can not be certain either that a single correct turn made by an animal in the maze proves that the animal has learned the turn, or that a single error proves the absence of the habit for the particular turn involved. The former may be due to chance, the latter to a distracting stimulus whose threshold of reaction is lower than that of the maze-habit. In a question of this sort the most dependable results are therefore to be obtained from averages, which rule out, to a certain extent at least, the chance successes and errors. It may be that while individual records do not show an exact progressive elimination of errors, the larger averages do reveal this as one of a number of factors influencing the course of learning. There is some doubt as to the comparability of the different alleys in the circular maze and no great significance can be attached to the progression except in the case of alleys b, c, d and e, which are strictly comparable.

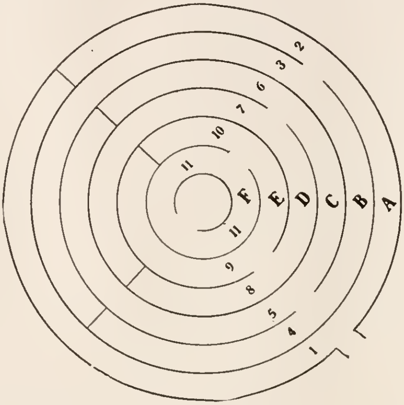

Figure 1.—Ground plan of circular maze, showing the position of the errors studied.

Vincent ('15, IV) has given data which indicates a more pronounced progressive elimination than appears in the work of Hubbert. In the form in which this is presented, however, Vincent is not justified in applying the data to the problem. She makes no statement as to what constituted a trial in her experiments and in the two " typical records " of trials which she reports in detail ('15, I) we find that the rat, after reaching the food, was allowed to return and re-explore the maze. In the first trial of her rat " No. 1 " the animal was allowed to leave the food compartment and explore the inner *cul de sacs* twice before the trial was ended, and in the second trial the animal left the food and explored the inner alleys five times. If the final data is based upon trials conducted with this technique it can have no bearing upon the problem of the elimination of errors, for we can not determine whether the smaller number of trials required for the elimination of the errors near the food box resulted from retroactive association or from the fact that additional trials in the inner part of the maze were ignored.

Additional evidence dealing with the question of retroactive association is now at hand and makes possible a more positive conclusion concerning its rôle in habit-formation than could be drawn before. The evidence consists of data upon the elimination of errors during the training of 56 rats in the Watson circular maze. The method of analysis differs from that employed earlier by Hubbert in that different types of errors are treated separately.

The ground-plan of the maze is given in figure 1. As will be noted, two chief types of error are distinguishable. The first of these (type I) is the passing of a doorway through which the animal should go. Errors of this type are marked with even numbers in the figure. The other (type II) is that of an incorrect turn after passing through the doorway. Errors of this type are given odd numbers in the figure. In addition to these types are errors of turning back upon the correct pathway. While common enough in the early part of training these errors are soon eliminated. In the 616 possible cases in the data examined only one was found in which an error of turning back followed the last error of types I and II in any alley (with the exception of *f*, which, being without a partition, permits only errors of turning back), so that they may be disregarded in any study which deals only with the last error made at each given point in the maze. In compiling the data any turn which carried the animal for its own length or more into a blind alley was counted as an error. Thus figure 2, a tracing of the path followed in a single trial, shows errors at 2, 5, 7, and 11. The records of all the animals were examined and note made of the number of trials preceding the last in which each of the 11 possible errors was made. The averages of these for the 56 rats are given in table 1.

TABLE 1

The Average Number of Trials Required by the 56 Rats for the Elimination of Each of the 11 Errors Possible in the Watson Circular Maze. The Numerals Indicate the Position of the Errors in Figure 1.

Errors of passing a door		Errors of turning wrongly	
Number	Average trials before elimination	Number	Average trials before elimination
2	30.07	1	36.62
4	23.19	3	36.48
6	19.18	5	37.97
8	12.48	7	39.21
10	21.05	9	32.46
Averages	21.19	Averages	36.55
Number 11			30.27

TABLE 2

The Number of Cases in Which Each of the Blind Alleys Was Not Explored Once Before the Maze-habit Was Thoroughly Established

Errors of passing a door		Errors of turning wrongly	
Number	Number of cases	Number	Number of cases
2	0	1	0
4	2	3	0
6	3	5	0
8	22	7	0
10	4	9	2
Total	31	Total	2

The most striking fact brought out by this table is that errors of type I are eliminated in less than two-thirds as many trials as are those of type II. Many rats never made certain errors and the distinction between the types is shown here also. Table 2 gives the number of cases in which each of the errors was not made once during the course of training. Blind alleys, entrance to which constitutes an error of type II remained unexplored in only two cases. In contrast to this, blind alleys beyond the doorways remained unexplored in 31 cases.

What is the explanation of this fact? The first suggestion is that there is a transfer of the reaction learned for one doorway to other situations, but it may be also that a break in the smooth walls of the alleys excites some instinctive mechanism which carries the animals through the doorways. To test this latter possibility the records were examined to discover whether the animals more frequently went through the first door that they came to in their first trial in the maze or passed beyond it into the blind alley. that is, whether or not error 2 was made at the first possible opportunity. It was found that, of the 56 records of first trials 32 showed that the animal turned through the first doorway and 12 that he passed the doorway. The remaining 12 were uncertain owing to the confusion of lines made in following the movements of the rats. Thus in three-fourths of the available cases the animals, without previous training, turned through the doorway instead of passing it; a fact which furnishes evidence for an instinctive basis for the elimination of errors of type I. It is probable that this accounts for the difference in time required for the elimination of the two types of errors.

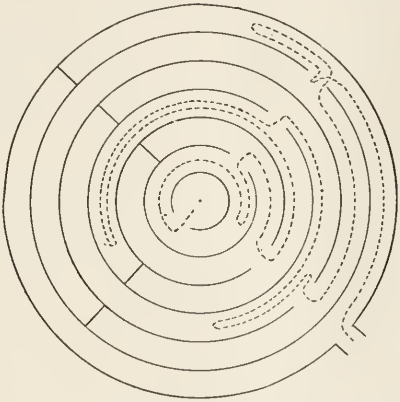

Figure 2.—Tracing of path followed in one trial, showing method of counting errors. Errors were made in this trial at 2, 5, 7 and 11.

An additional difference between the types of errors, which is not explained by instinctive behavior, is the order of elimination within the series. Among the errors of type I there is a very marked reduction in the number of trials required for the elimination of successive errors from the circumference to the center of the maze. Nothing of the sort is apparent in errors of type II.[3] Is there a retroactive association in the case of errors of type I and not of type II? If such association, in the sense of a serial formation of conditioned reflexes, is an important principle in habit-formation it must be obscured by other agents in the elimination of errors of the second type. If not, it is for some reason simulated in the elimination of errors of type I. An inquiry into the relative complexity of the factors influencing the elimination of the two types of errors gives data which seems to favor the latter possibility. Movements toward the center of the maze are much more influenced by gross orientation than are those of turning to the right or left. After the third to sixth trial the rats run with their heads near the convex (inner) walls of the alleys of the maze and almost invariably confine their efforts to climb out of the alleys to these partitions. Such behavior becomes more pronounced as they approach the center of the maze and persists until the limits of training are reached. It is improbable that this is a reaction to the odor of food in the center of the maze, first, because it does not occur during the first trials and second, because smearing the maze with food does not alter the reaction essentially. It may be a reaction to the curvature of the sides of the alleys but such an association seems improbable in view of the slowness with which similar sensory habits are formed in the discrimination box. The final alternative is that of an orientation to the maze as a whole. The work of Carr shows that the animals are usually well oriented with respect to the direction of the food compartment from the starting box and may even depend upon the direction of the maze from their home cages for orientation. The behavior of the rats strongly suggests that they very soon acquire this sense of direction in the maze and that as they approach the center of the maze the orientation becomes more certain, perhaps by the summation of familiar stimuli, perhaps by the closer approximation of the visible objects above the maze to their appearence from the food-box.

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[3] There is good reason for disregarding the two errors which are not in conformity with the others, errors 10 and 11. After reaching the food at the center of th- maze the rats frequently turn back and explore the inner alleys of the maze before eating. These exploratory activities constitute one of the most characteristic instinctive activities of the rat. In the home cages they are usually not evident in the scramble for food which takes place when several rats are together in a familiar place, but in all relatively new situations the animals rarely begin to eat until they have made a thorough exploration of their surroundings. In the maze the field of exploration usually includes the food compartment, the alley *f*, and its doorway which leads to error 10. When the rats have learned the maze they may eat as soon as they reach the food, but any strange odor or startling noise may lead to a re-

The conditioning stimuli to an orientation determined either by the curvature of the alleys of the maze or by the visible

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tracing of this part of the path. This is evidence for an additional interfering agent in the elimination of errors 10 and 11 which does not act in the case of the other errors and justifies the view that the elimination of these errors is not directly comparable with that of the others. In the experiments reported here every effort was made to prevent this retracing of the path. The moment the animal entered the food-compartment the experimenter hastened to close the doorway between alleys *e* and *f*, and in very few cases did the rats escape into the outer alleys.

objects above them, would obviously remain nearly constant, no matter in what alley the animal happened to be. A similar orientation with respect to right and left turns could not be maintained equally well because the direction of the doorways alternates with successive alleys. We have not had opportunity to test the mechanism of orientation but there can be little doubt that the elimination of errors of type I is affected by it to a greater extent than is that of errors of type II. We can find, on the other hand, no evidence for any influence which might hide a retroactive association in the elimination of errors of type II. Such an influence would have to be equally strong and equally uniform in its action with retroactive association and the behavior of the rats gives no evidence of anything which might produce this result.

Whatever the explanation of the serial elimination of errors of type I, the process is evidently a complicated one and can not be advanced as proof of retroactive association. No such complication can be demonstrated in the elimination of errors of type II. They show a pronounced uniformity in the amount of practice necessary for their elimination; a greater uniformity than should be expected if chance agents obscured the effects of retroactive association, and it seems certain that their elimination presents a purer case of learning by the method of trial and error than does that of type I. The number of animals is large enough to make the averages dependable while still allowing as great a chance variation as is found between the averages in type II. Clearly the principle of retroactive association does not apply to errors of this type.

Since, as we have pointed out, the elimination of this type of error is probably not complicated by transfer of training from one part of the maze to another, by orientation toward the center of the maze, or by reactions to the curvature of the passages, etc., we may extend our conclusion and say that retrogressive association is not an effective mechanism in the selection and association of simple series of motor activities in habit-formation.[4]

Evidence for the absence of retroactive association does not, of course, throw much light upon the physiological mechanism by which the getting of food fixes the habit. It indicates that this is not the formation of a series of conditioned reflexes such as was outlined in the first part of the paper. It suggests further that the same mechanism is involved in learning *similar* reactions in different parts of the maze and that the rate of learning is the same irrespective of the temporal relation of these to the getting of food.

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[4] Here and elsewhere in this paper the word "association" is used to express merely the production of a new temporal relation of stimulus and reaction.

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A CAUSAL FACTOR IN THE RELATION OF THE DISTRIBUTION OF PRACTICE TO THE RATE OF LEARNING

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The fact is well established that, within limits as yet undetermined, the rate of learning varies inversely as the concentration of the periods of practice. A number of hypotheses have been advanced to account for this but none of them has any experimental evidence in its support. One of them, offered by Book[1] to account for improvement in typewriting during periods of non-practice, assumes that during a long period of practice the learner may acquire certain habits which, persisting through the practice-period, limit his chance activities and hence his possibility of improvement by the method of trial and error. During rest-periods these habits, which are not very well established, may be lost, in which case a distributed practice would permit of a greater diversity of activity than a concentrated one. In other words, during a long period of practice the learner is apt to get into a rut and intervals of rest permit him to return to the problem with a new " set " and to attack it in a different way.

The hypothesis applies not only to the periods of non-practice dealt with by Book, but to any of the effects of the distribution of practice. If it is correct, a detailed analysis of behavior in the formation of any habit should show a greater diversity of activity between successive practice-periods than within single periods. In my experiments upon the acquisition of skill in archery I observed the persistence of bad methods of aiming through single periods of practice but, lacking time for detailed descriptive or photographic records, was unable to determine the rôle of these in modifying the effects of practice.[2]

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[1] The Psychology of Skill: with special reference to its acquisition in typewriting. Missoula, University of Montana, 1908.

[2] Acquisition of Skill in Archery. *Carnegie Pub.* 211. 1915.

A simple method of recording significant motor activities for a study of this problem is offered by the graphic maze.[3] With it records are obtainable of all the errors made by the animals being trained and it is easy to determine whether or not any of the errors persist through single periods of practice or from day to day. If such persisting errors are the real cause of the results obtained with different distributions of practice, one should expect to find, on the average, fewer errors common to the last trial of one day and the first trial of the succeeding day's practice than to any two successive trials made on the same day.

Comparison of the numbers of duplicate errors can not be made directly owing to variations in the number of errors made in different trials and the consequent difference in the probability of chance duplication.[4] Thus if nine out of a possible twelve errors are made in each of two successive trials a larger percentage of identical errors is to be expected from pure chance than if only three errors are made in each trial. In making the comparison I have used the records of all the errors made by 56 rats in learning the circular maze, when given five trials daily. To avoid the influence of different numbers of errors in the comparison of the number of duplicate errors appearing in single and successive practice-periods the following method of computing the results was adopted.

The records of the last trial in each day's practice and of the first in the succeeding one, where a total of three or more errors appeared in the two trials, were compared and the number of errors in each, together with the number of duplicate and diverse errors, was tabulated. The records of the animal which furnished this data were then examined for a case of two successive trials on the same day each of which contained a number of errors equal to that in the corresponding trial of the pair made on successive days. The first pair of trials meeting these requirements was taken for comparison and its numbers of duplicate and diverse errors were arranged in a separate table. Where no pair could be found which met the requirements the successive trials in different practice-periods were discarded.

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[3] Yerkes and Kellogg. A graphic method of recording maze reactions. *Jour. Animal Behav.*, 1914, **4**, 50-55.

Watson. A circular maze with camera lucida attachment. *Ibid.*, 56-59.

[4] The methods of training animals and recording errors in the maze have been described so frequently that they need not be discussed here. The reader who is unfamiliar with the methods is referred to J. B. Watson, "Behavior," 1915.

One hundred seventy-five pairs of successive trials made in different periods of practice with an equal number of pairs made during a single day's practice were obtained. The method gives essentially a random sample of the two kinds of pairs of successive trials, with an equal number of errors and an equal distribution of errors between the members of the pairs of each series. The rôle of chance in the production of duplicate errors may therefore be disregarded, since it should be the same for both kinds of pairs, and the relative proportion of duplicate to distinct errors in the two kinds of pairs may be considered the result of the time intervening between the successive trials. In computing the errors wrong turns only in the maze were considered and only one error was counted at each turn where errors were made. The results of the analysis are given in the following table. The totals of all cases are given and the figures for the numbers of diverse and duplicate errors are directly comparable, being based upon the same number of errors with like distribution between the pairs of trials.

SUCCESSIVE PRACTICE-PERIODS

Total number of errors in last trials of first practice-periods	463
Total number of errors in first trials of succeeding practice-periods	524
Total number of *pairs* of identical errors	247
Total number of diverse errors	493

SINGLE PRACTICE-PERIODS

Total number of errors in first trials of pairs corresponding to those above	463
Total number of errors in succeeding trials of pairs corresponding to those above	524
Total number of *pairs* of identical errors	274
Total number of diverse errors	439

In both kinds of pairs the number of duplicate errors is slightly in excess of the number of diverse ones. The maze, as arranged, offers the possibility of 12 different errors and the average number of errors per trial was 2.82. The chances, then, that the number of duplicate errors would equal the number of diverse errors was only about one to eight. The fact that the numbers were equal when the data included so many cases seems to prove that there is some predetermining factor which causes errors once made to be repeated both in single practice periods and from one practice-period to the next.

A comparison of the pairs of trials made during the same period of practice with those made in successive periods shows a greater diversity of errors in the latter. In them there were 247 pairs of like errors and 493 diverse errors; that is, 49.05% of the errors made in successive trials were diverse. In the successive trials made on the same day there were 274 pairs of like errors and 439 diverse errors; 44.48% of the errors made in these successive trials were diverse. The trials separated by a 24 hour interval are thus seen to include 10% fewer duplicate errors than those without intervening time: a greater diversity of activity occurs where successive trials are separated by a considerable interval of time than where they follow each other immediately.

This is the result to be expected on the hypothesis considered above and it seems to place the latter on a firm basis. Two questions, however, are unanswered: first, is this the only factor involved in producing the results noted when different distributions of practice are used; second, is the hypothesis applicable to other types of activity than motor forms such as archery or typewriting. It is not possible at present to say how great would be the effect of the conflicting habits in retarding the rate of learning in any particular case. If the diversity of activity is reduced 10% by the concentration of practice from one to two trials per day, a 10% increase in the amount of practice necessary for learning is the least which could be expected, but the fact that the disadvantageous activities are repeated more frequently with increasing concentration of practice would help to fix them as habits and thus produce an even greater retardation of learning. At a rough estimate, the persistence of the same errors through prolonged periods of practice seems adequate to account for such retardation of learning as has been found to result from concentrated practice during the formation of motor habits.

If the same explanation is not applicable to language habits, its validity for motor habits is questionable. In view of our ignorance of the mechanism of association in such activities generalizations here must be made with caution. There can be little doubt, however, that false associations occur in the formation of language habits and it seems probable that these may interfere with learning in the same way that habits of making wrong turns in the maze interfere with the learning of the correct path.

THE COURTSHIP OF *PIERIS PROTODICE*

PHIL RAU

The mating habits of *Pieris protodice* have been so uniform in all of the cases which have come under my observation in various times and places that I feel that this phase of their behavior is fairly constant. The following cases are typical of the usual performance.

On June 12, at 5:10 p. m., many of these white butterflies were fluttering about one of their favorite haunts, a patch of white-flowered milkweed in a sunny, treeless pasture. A female was at rest on the upper surface of a leaf, with its wings spread flat and its abdomen turned directly upward into the air and held thus rigidly. A male was hovering above her with more than usual activity; frequently he would flutter very near to the upturned abdomen. Presently he grew more bold; he repeatedly approached and beat his wings against hers with a flapping motion, and darted toward her and touched her abdomen with his own, apparently in an attempt to mate, until the excitement grew intense after several such advances, and both arose on the wing and fluttered and danced and fussed in an almost quarrelsome manner in mid-air for a few seconds, when the female settled to rest on another leaf nearby in the very same position, and the whole performance was repeated. When the male again became too familiar the female flew away as before, the male following and the two fluttering 'round and 'round each other, high in the air. Then the coquettish female suddenly darted away and hid under a leaf near the ground, this time eluding her suitor.

Although there were hundreds of these white butterflies flying about and feeding upon the white flowers, only three pairs were in copulo. Perhaps the late hour in the day might account for the small number in mating.

On three occasions I chanced to see the beginning of this strange performance, but I was unable to ascertain at any time which sex made the first advance in this courtship. In each case the female was feeding or resting on the flowers, with closed wings in a normal, placid manner in so far as I could see, when the male came dancing by on the wing. As he approached and fluttered above her she promptly assumed the strange position described above, the wings spread flat and directed slightly backward, and the abdomen upraised. In each case they flirted until the excitement became riotous and then they fluttered away and must have separated, for they were lost among the many others in the field. I have never seen the accomplishing of actual mating, but in the several pairs observed already in copulo they rested tail-to-tail. When disturbed they would fly thus, in pairs. One pair continued flight for two and one-half minutes without alighting. The leader (sex not ascertained) did all the flying and seemed merely to carry the rear one.

On one occasion the pair continued their coquetry for fifteen minutes, with several attempts at mating. During this period the female moved from flower to flower, not with an air of trying to escape, but rather leading him on; the male persistently followed her, constantly on the wing and in a state of high agitation. Finally he knocked her to the ground, where he followed her still, and fell beside her, but he seemed exhausted and did not try to mate, but lay as if spent. The female, when she found she had exhausted him, arose on the wing and flew lightly and indifferently away.

A pair in copulo were quietly at rest on a low shrub. I picked them up in the fingers for examination and soon replaced them, but after such disturbance they separated and went flying and fluttering about each other, over the clay bank, over the stream, over the low plants for about seven minutes, when they settled for an instant and I thought they would reunite. But the female dropped several inches to a lower stratum of leaves, remained there for a few seconds and then darted away. I expected the male to go in hot pursuit; instead, for the next ten minutes, while the female was dancing over some shrubs a hundred yards away this male was frantically going in and out among the leaves in the spot on the lower stratum where the female had paused for a few seconds. It was pathetic to see his eager search; the only spot that seemed to have an attraction for him was the place where the female had been, even though he had not seen her drop to it, but had only located the spot after she had left it. As the male hunted frantically about her former location, while the female was dancing in full view, I could not help but feel convinced that in this case at least the sense of sight was inferior to the sense of smell.

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THE DISTRIBUTION AND ELIMINATION OF ERRORS IN THE MAZE

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In the solution of the maze problem, animals do not distribute their errors equally between the various cul de sacs; apparently these blind alleys do not offer equal incentives to entrance. Neither do the cul de sacs present the same difficulty in mastery; the tendency to enter certain alleys is eliminated much sooner than in the case of others. The principles determining the relative frequency of entrance into the various alleys, and the factors governing the order of their elimination are inadequately known.

Vincent[1] has published data concerning the first problem. Hubbert[2] and Vincent[1] have investigated the second question, and Watson,[3] on the basis of Hubbert's results, has contributed to the discussion.

Watson contends that if food satisfaction is a causal agency in selecting the true path and thus eliminating the cul de sacs the latter part of the maze should be mastered first; hence the cul de sacs should be eliminated in the order of their nearness to the food box. He therefore concludes that food satisfaction can not be regarded as a selective agency because only seven of Miss Hubbert's eighty-four rats eliminated the six errors in the exact order of their spatial contiguity to the food box.

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[1] Vincent. The White Rat and the Maze Problem. *Jour. Animal Behav.*, **5**, 367-374.

[2] Hubbert. Elimination of Errors in the Maze. *Jour. Animal Behav.*, **5**.

[3] Watson. Behavior, p. 268.

Watson's argument, to my mind, contains two fallacies: 1. A causal factor can mediate an invariable result (without any exceptions) only under the ideal condition that it is the only causal agency involved. Needless to say such a condition does not obtain in any science, to say nothing of animal behavior. The ideal effect of any hypothetical cause is always somewhat altered, distorted, or even obscured by the influence of other factors which can not be controlled. Hence general tendencies and results must be utilized as diagnostic symptoms in the search for causal conditions. Viewed in this light, Hubbert's results support rather than disprove the efficacy of the alleged principle of selection, for the general trend of the order of elimination is that of the spatial contiguity of the alleys to the food box. According to my computations, 80% of her rats eliminated the 6th error before the 5th, 50% the 5th before the 4th, 47% the 4th before the 3rd, 73% the 3rd before the 2nd, and 70% the 2nd before the 1st. Determining the average number of trials necessary to eliminate each cul de sac, the order of elimination for the entire group was 6-5-3-4-2-1, where the successive errors are numbered in order from the entrance. This order gives by the rank method a positive correlation of .943 between quickness of elimination and propinquity to the food box. The average number of trials necessary to eliminate the last three errors was less than that for the first three for 90% of the rats. Surely there is a very pronounced tendency for the errors to be mastered in proportion to their nearness to the food box, and the deviations from an *exact* correlation for each rat may well be due to the operation of other causal agencies. The existence of other efficacious agencies, viz., recency and frequency, is admitted by Watson. 2. Granted that food satisfaction is the only effective agency involved, yet a *perfect* correlation between speed of elimination and nearness to the food box, as demanded by Watson, would not obtain. According to the hypothesis the order of elimination will be determined, not by the spatial arrangement of the cul de sacs in relation to the food box, but by the temporal relation of the errors to the food experience. The temporal order in which the cul de sacs are entered is not the same as their spatial order in the maze. Not all cul de sacs are entered on each run. An animal may enter alleys 1, 3, and 5, and skip 2, 4, and 6. The matter is further complicated by the phenomenon of returns. The tendency to return toward the entrance box is very persistent during the early stages of learning, and in any trial we may have a temporal order of 1-3-6-1-2-3-4-5-4. According to the hypothesis this trial will tend to eliminate alleys 3, 4, and 5 prior to 6.

Hubbert's results, however, neither prove nor disprove the efficacy of food satisfaction as an eliminative agency. Although a high degree of correlation obtains between rate of elimination and nearness to the food box, one should still refrain from generalizing on the basis of one maze. Different maze patterns may give other results. A correlation between two factors does not always indicate a causal relation between them; both may be the result of some more fundamental condition.

This paper presents data on two mazes, and in addition Miss Vincent has kindly furnished me records for six mazes. A cul de sac was considered eliminated when but one entrance was made in ten successive runs. The number of trials necessary to eliminate each alley was determined for each animal and the average number of trials for the group was thus computed for the various cul de sacs. These values constitute the order of elimination for the group. This temporal order of mastery was correlated by the rank method with the spatial arrangement of the alleys in relation to the food box. Table I designates the various mazes, gives the number of cul de sacs in each, the number of rats employed, and the correlation data for each maze pattern. Mazes I-a to I-e have the same pattern, a slight modification of the Hampton Court arrangement; they differed only in the arrangement of sensory factors. I-a presented a uniform sensory interior; I-b had the true path painted white and the blinds black; I-c had the true path painted black and the blinds white; in I-d an olfactory trail was laid in the true path, while the trail was inserted in the cul de sacs for I-e. II-a and II-b were alike except that the alleys of II-b were without sides. The records for the above mazes were obtained by Miss Vincent. Mazes III and IV were somewhat similar in pattern but radically different from patterns I and II. Maze V refers to the circular maze used by Miss Hubbert whose data are given for comparison.

TABLE I

Correlation Between Quickness of Elimination and Nearness to the Food Box

Maze	Number of cul de sacs	Number of rats	Percentage of correlation
I-a	7	10	.607
I-b	7	10	.714
I-c	7	9	.178
I-d	7	6	—.643
I-e	7	6	—.358
II-a	7	6	.750
II-b	7	6	—.822
III	11	16	.563
IV	9	15	.666
V	6	84	.943

Varying degrees of positive correlation between the two factors were obtained for six of the nine mazes. None of our values are as high as that obtained for Miss Hubbert's maze. There are, however, three exceptions to a uniform positive correlation; in these three mazes the errors were mastered in proportion to their nearness to the maze entrance. This lack of a uniform positive correlation can be interpreted in two ways. 1. If food satisfaction is an effective agency of elimination, its influence is overcome by some other selective factors which are peculiar to three mazes. 2. On the other hand we may suppose that food satisfaction is non-effective and that all of the above correlations (both positive and negative) are to be explained in terms of a single principle. The latter hypothesis is the preferable one.

Miss Vincent suggested in her paper the possibility that the ease of elimination is a function of the strength of the tendency to enter an alley, and that in a general way the relative attractiveness of the various alleys can be measured by the frequency with which they are entered. Cul de sacs with the greatest error score offer the most inducement to entrance, and the stronger the attraction, the larger will be the number of trials necessary for elimination. On this basis a negative correlation will obtain between the number of errors for each alley and the order of mastery. To test the hypothesis, the various cul de sacs were now ranked in the order of number of entrances made by the group for the successive stages in the mastery of the maze. Correlation data were computed by the ranking method with much detail but since these results were uniformly consistent for all stages of learning, we give in table II the values for representative stages. The first horizontal column states the correlation values for the various mazes between the order of elimination of the alleys and the relative number of entrances made by the group as a whole for the first trial. The second column gives similar data in relation to the total number of errors made during the second and third trials. The last three columns state the results in reference to the total number of errors made in the first five runs, the second five runs, and from the eleventh trial until the maze was mastered.

TABLE II

Correlations Between Quickness of Elimination and Number of Errors at Different Stages of Learning

Trials	I-a	I-b	I-c	I-d	I-e	II-a	II-b	III	IV
1	–.571	–.821	–.535	–.714	–.892	–.321	–.642	–.654	–.133
2- 3	–.535	–.643	–.892	–.857	–.643	–.107	–.321	–.300	–.166
4- 5	–.642	–.571	–.821	–.535	–.500	–.642	–.964	–.764	–.350
1- 5	–.714	–.892	–.750	–.857	–.857	–.143	–.642	–.758	–.116
6-10	–.857	–.857	–.678	–.750	–.857	–.857	–.571	–.518	–.583
11-until learned	–.500	–.785	–.857	–.535	–.321	–.928	–.000	–.973	–.866

With one exception, a uniform negative correlation was obtained, the values ranging from —.107 to —.964. The exception refers to the final stage in the mastery of maze II-b. This record hardly invalidates the uniformity of the results as this maze was mastered very easily and but few errors were made after the tenth run. In considering the validity of this correlation, the uniformity for all mazes and for the various stages of learning must be emphasized. A single correlation value may well be due to chance in view of the paucity of data for which the correlation was calculated. But chance is pretty well eliminated when the computation is repeated 54 times and consistent results are secured. We may then safely conclude that some degree of negative correlation obtains for all stages of learning between quickness of elimination and the tendency to enter the cul de sacs, that in a general way those blind alleys which for some reason offer little inducement to entrance are easily eliminated, while cul de sacs which present the most enticement to exploration are the hardest to master. This correlation is *a priori* logical, for it is reasonable to expect that the strongest tendencies will be the hardest to overcome. Our results thus establish one of the factors underlying the order of error elimination, viz., that this order is a function of the strength of the entrance attraction characteristic of the various cul de sacs. It is admitted that other selective factors may also be efficacious; otherwise higher correlation values should have been obtained.

The validity of the above principle of explanation is supported by the data of table III, giving the correlation values between the number of errors for the various cul de sacs and their spatial order in the maze. A positive correlation obtains for the six mazes I-a, I-b, I-c, II-a, III, and IV. In these cases the animals entered the various cul de sacs with a frequency roughly proportionate to their proximity to the point of entrance, and it was for these six mazes that a positive correlation was found between order of elimination and nearness to the food box (table I). In other words the first cul de sacs were entered the most frequently and were the last to be eliminated. In mazes I-d, I-e, and II-b, on the other hand, the animals for some reason entered the last cul de sacs more frequently than the initial ones (negative correlation between number of errors and nearness to entrance), and in these cases the final errors were the last to be eliminated (table I).

TABLE III

CORRELATIONS BETWEEN NEARNESS TO ENTRANCE AND NUMBER OF ERRORS AT DIFFERENT STAGES OF LEARNING

Trials	I-a	I-b	I-c	I-d	I-e	II-a	II-b	III	IV
1...........	.322	.929	.822	–.964	–.107	.000	–.607	.846	.750
2- 3...........	.250	.679	.036	–.928	–.107	–.392	–.214	.709	.666
4- 5...........	.232	.143	.215	–.321	–.750	.143	–.892	.373	.800
1- 5...........	.322	.715	.679	–.928	–.214	–.107	–.607	.846	.700
6-10...........	.286	.786	.643	–.250	–.500	.465	–.107	.573	.733
11-until learned..	.215	.250	.179	–.285	–.071	.536	.393	.500	.417

It is thus the phenomenon of error distribution in the maze that demands explanation in order to comprehend the order of elimination. Our results enable us to offer but few explanatory suggestions in regard to error distribution.

1. The persistent tendency for rats to keep returning to the point of entrance after exploratory excursions operates to increase the number of entrances into the initial cul de sacs. This returning tendency is well known, and it is at once obvious that these returns must result in repeated explorations of the initial

cul de sacs. All other factors being equal, we should expect that the relative number of entrances into the various cul de sacs will be roughly proportionate to their nearness to the point of entrance. This influence of returns is further indicated by two features of the data: a. In mazes I-d and I-e there is a negative correlation between number of errors and nearness to the entrance, the greater number of errors being made in the final cul de sacs (table I). The opposite relation, however, obtains for mazes I-a, I-b, and I-c, in which the greater number of entrances were made in the initial cul de sacs. This difference in the distribution of the errors among the cul de sacs is due entirely to differences of the sensory character of the mazes, for exactly the same maze pattern was used throughout and the objective environment of the mazes was identical in all cases. Mazes I-d and I-e differed from the others in that an olfactory trail was laid, either in the true pathway or in the cul de sacs. This trail produced several characteristic peculiarities of behavior, one of which was a noticeable diminution of the number of returns. Miss Vincent kept no separate record of the number of returns, but she noted this feature of the behavior and frequently discussed its significance with the writer at the time. The degree of returning also accounts for the different distribution of errors in mazes II-a and II-b (table III). Again the same pattern was used and the maze was located in the same objective environment in both experiments. The only difference consisted in the presence and absence of sides to the runways. Maze II-b was without sides and their absence caused the animals to follow one edge of the platform with their paws or vibrissae much in the same manner as did the olfactory trails. Following an edge caused a noticeable diminution in the number of returns and thus accounts in part for the difference of error distribution in the two mazes. b. The returning tendency is quickly eliminated in the course of maze mastery, and we should thus expect that the relative frequency of entering the initial cul de sacs will be gradually diminished during learning for those mazes in which returns are an effective factor in error distribution. Such a diminution obtains for mazes I-a, I-b, I-c, III and IV (table III). In all five cases there is a high positive correlation between number of errors and nearness to the entrance, but this correlation keeps decreasing with the number of trials; in other words the number of errors in the initial blind alleys is decreased more rapidly than for the final cul de sacs.

2. The sensory character of the maze influences the distribution of errors in other ways than by minimizing the number of returns. The tendency to follow the edge or an olfactory trail evident in mazes I-d, I-e, and II-b operated to reduce the total number of errors. This fact is well demonstrated in Miss Vincent's paper. The operation of the tendency was relatively more effective in the initial than in the final stages of learning, and Miss Vincent interpreted this fact as due to the shift in control from olfactory and cutaneous cues over to kinaesthetic factors; when the maze is run in terms of kinaesthetic stimuli, the trail factor is no longer present and the rat is subject to the enticements of curiosity, distractive odors, etc. I wish to suggest a similar explanation of the greater frequency of entrance into the final cul de sacs in these three mazes. Starting from the entrance box, the rats are at once dominated by the stimulus characteristic of the trail. This sensory trail is followed and possible exploratory excursions due to curiosity, fear, and other motives are eliminated. As a consequence relatively few errors are made in the first sections of the maze. As the final sections are reached, however, the dominance of the trail motive is weakened and other enticements begin to operate. The weakening of the trail motive may be conceived under such terms as habituation or adaptation. The strength of other motives such as fear, curiosity, and the returning tendency may progressively increase with the distance traversed; the concept of summation of stimuli may be applicable here. The strength of the olfactory stimulus from the food box must necessarily increase as the final sections of the maze are reached. One can hardly suppose that the actions of an organism so complex, alert, variable, and thoroughly alive as is the rat can long be continuously dominated by a single motive. Some shift of motives during a run must be presupposed irrespective of the explanatory difficulties involved. Our hypothesis then assumes that the animals in these three mazes start out on each run under the dominance of the trail motive which tends to prevent errors. As the final section of the maze is reached, there occurs a shift of motives, and these new motives, such as food odor, fear, curiosity, etc., tend to produce errors. As a consequence of this shift of motives

during each run the greater number of errors will be made in the final cul de sacs in these three mazes. It is also possible that the same principle, a shift of motives, will account for the greater frequency of entrance into the initial cul de sacs in the normal mazes; in this case the shift will be from fear and curiosity over to the food odor. The odor of food as the rat reaches the final sections should be sufficiently directive as to minimize the number of errors relative to those made when the animal's acts are controlled primarily by curiosity and caution.

3. The distribution of errors is influenced by certain peculiarities of the cul de sacs other than their positional relation to the point of entrance. Since the influence of this factor may vary according to the stage of mastery, a separate treatment is necessary for its effects upon the initial and final distribution of errors.

a. *Initial distribution.*—From the data of table III it is obvious that the initial errors (first five trials) are never distributed in the exact order of the spatial arrangement of the cul de sacs. A few blind alleys are generally responsible for the deviations, and these are listed in table IV. The first columns give the various mazes with the number of cul de sacs belonging to each. Each cul de sac is numbered in order from the point of entrance. In the column headed " plus " are listed those alleys in which the number of entrances exceeds that to be expected on the basis of a perfect correlation. In the " minus " column are those alleys in which the number of entrances is less than the normal. The first group of mazes are those in which a positive correlation obtains between the distribution of errors in the first five trials and the proximity of the cul de sacs to the point of entrance. In the last group of mazes the initial errors are distributed proportionate to the spatial contiguity of the cul de sacs to the food box. The five mazes, I-a, I-b, I-c, I-d, and I-e, are identical in pattern; in the first three the sensory conditions were such that the greater number of errors were made in the initial cul de sacs; in the last two, the first cul de sacs were the least attractive. In spite of this radical difference of error distribution in the two groups, the same cul de sacs are responsible for the deviations from a perfect correlation in every case. The first cul de sac is much less alluring in the initial trials than its position would justify. On the other hand No. 6 was invariably attractive for it was entered much more frequently than one would expect if the spatial order of the cul de sacs were the only factor determining the distribution of errors in the initial trials. Likewise No. 3 was relatively difficult in two cases, and No. 4 three times. Comparing mazes II-a and II-b of like pattern but with a different distribution of errors, we find that No. 7 is easy in each case while No. 4 tends to be difficult. Chance will account for the deviations in part, but chance can not invariably favor certain cul de sacs. The tendency toward uniformity in the character of the deviations for the same maze pattern must be due to peculiarities of the cul de sacs other than their spatial position in the maze. Certain ones are relatively easy to avoid, while others are prone to be entered.

The susceptibility of the animals to these favored cul de sacs is, however, an individual matter. In maze III, No. 8 received more than its due share of entrances, yet this alley was not entered at all in the first five trials by four of the sixteen rats; in fact one animal did not enter this alley once in fifty trials, while another rat entered but three times in fifty runs. This avoidance of the difficult errors by certain rats can in part be explained in terms of the habits acquired by those animals in traversing the first section of the maze. Let us suppose that the first section of a maze contains no blind alleys but consists of a series of runways so arranged as to necessitate alternating right and left turns of 90°. At the end of this section there is presented a choice between two paths,—a " straight ahead " error, and a turn of 90° leading to the food box. It is conceivable

TABLE IV

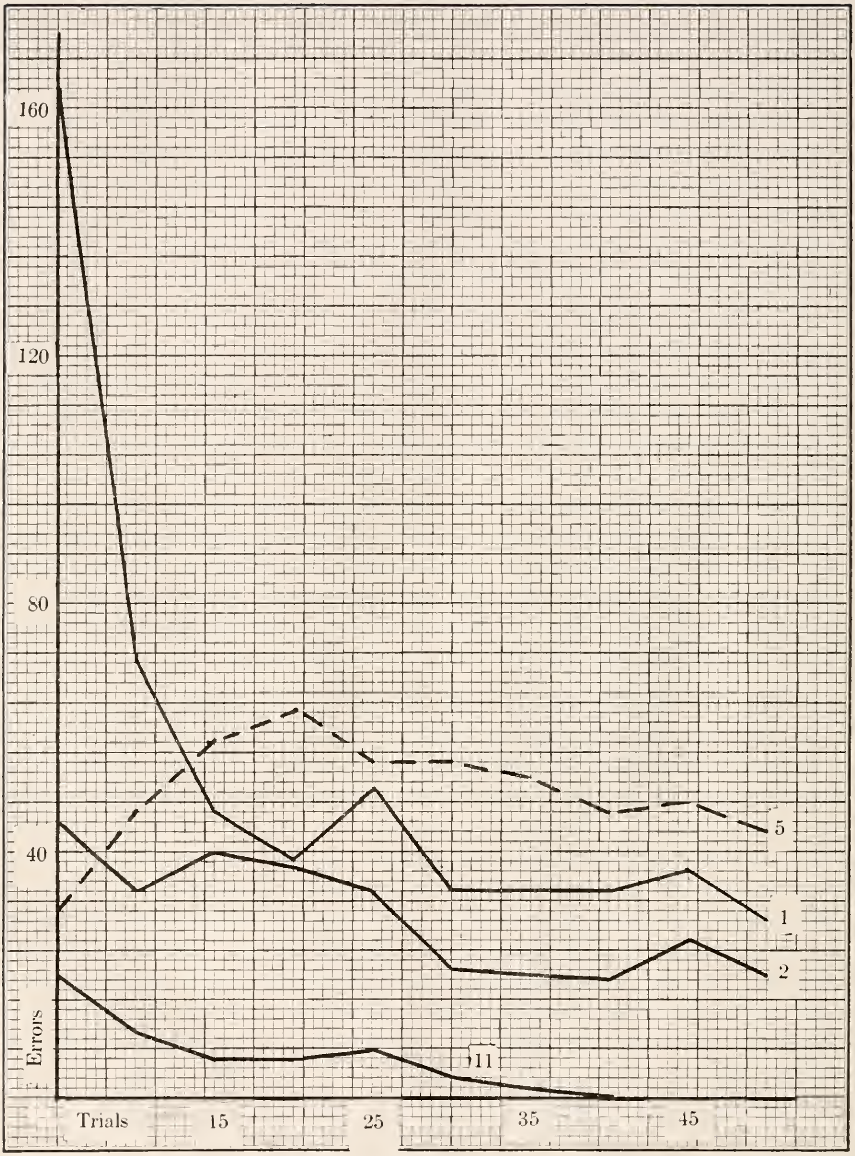
Deviating Cul de Sacs

Maze	Number of cul de sacs	Plus	Minus
	A. Mazes exhibiting a positive correlation		
I-a	7	3, 6	1
I-b	7	4, 6	1
I-c	7	4, 6	1, 2
II-a	7	4	1, 2, 3
III	11	8	7, 10
IV	9	3, 4, 8	6
	B. Mazes exhibiting a negative correlation		
I-d	7	3, 6	1
I-e	7	3, 6	1, 5, 7
II-b	7	4, 6	3, 7

that a choice between two such possibilities might be determined to a large extent by tendencies aroused in traversing the previous zig zag course. On this hypothesis the attractiveness of any cul de sac in a maze is in part a function of the motor tendencies developed in the prior sections of the maze. The habits aroused in a group of individuals in traversing the initial section of a maze must necessarily have much in common, and yet any part of a maze presents possibilities of wide divergence in the character of the pathway actually traversed. A group will thus approach a cul de sac with some degree of uniformity of disposition toward it, but radical exceptions are possible.

b. *Final distribution.*—The final distribution of errors represents the order of elimination, for eliminated cul de sacs are those which are not entered. As previously developed there is a correlation between the initial distribution of errors and the order of mastery of the blind alleys, but this correlation is far from perfect. It is thus evident that the order of elimination, or the final distribution of errors, is also dependent upon other factors than initial attractiveness. Certain peculiarities of the cul de sacs constitute a determining condition. Some blind alleys are relatively difficult and others are relatively easy to master, and this ease or difficulty of a cul de sac is to some extent independent of its initial attractiveness.

The above principle is well illustrated by mazes III and IV. The eleven cul de sacs of maze III fall into four rather well defined groups as to rate of elimination. The progress in mastery of four cul de sacs typical of these groups is represented by the curves of fig. 1. The alleys chosen as types are 1, 2, 5, and 11. The values represented are the total number of errors made by the group for each successive five trials. Curves 1, 2, and 11 illustrate the first principle that the order of mastery is inversely proportionate to the number of initial errors. No. 11 elicited but few initial errors and was mastered first; No. 1 was the most attractive but the most difficult, while No. 2 occupies a median position between the two. As to progress of mastery the three alleys are to be ranked in order, 1, 2, and 11. No. 5 is the exception which illustrates the influence of the second factor. This cul de sac was the hardest of the eleven to master, and yet its initial attractiveness was no greater than its position would justify. The number of entrances into this alley rapidly


160
120
80
40
Errors
Trials
15
25
35
45
5
1
2
11

increases for the first fifteen runs, and then slowly decreases for the remaining thirty-five trials. More errors were made at the end of the experiment than at the beginning. In considering the individual records, the general features of the group curve are also characteristic of that of fifteen of the animals. In maze III, the difficult group of cul de sacs is composed of alleys 5, 7, and 8. In maze IV, alley 3 was relatively easy while 5, 6, and 9 were the difficult ones.

This difficulty of any cul de sac must be explained mainly in terms of the animal's organization in reference to it, for all of the blind alleys of mazes III and IV were highly uniform in character. Each consisted of a single straight runway sixteen or twenty inches long. This reduction of the difficulty of a cul de sac to the animal's disposition toward it allows of a common explanation for both the initial and final distribution of errors. The disposition of an animal to enter or avoid an alley is a result in part of the habits of turning already developed. As the maze is mastered, these habits become profoundly modified. Returns and repeated explorations are inhibited and several cul de sacs may be eliminated. Since the attractiveness of a cul de sac is a function of the maze habit and this habit is altered in the course of mastery, it is evident that the initial and the final attractiveness of an alley must be to some extent independent variables. With this conception the disposition to enter an alley may actually increase as well as decrease, and individual exceptions to the group attitude are possible.

Such an explanation is feasible and the conception possesses some degree of *a priori* rationality, but any convincing proof of the hypothesis is more difficult. Chance can not account for the error curve of alley 5 in fig. 1, for the records of fifteen of the sixteen animals conform to its general features. There has been no objective change in the alley itself. Evidently it is the attitude of the animals towards this situation that has been altered. Nor will chance account for the distribution of errors of any individual animal. One rat did not enter alley 5 during the first five runs but made one entrance per trial for the remaining 45 runs. Another animal avoided this alley for eleven runs, alternated between success and error for the next six trials, and the error then became fixed. In another case this cul de sac was avoided twice, entered once, avoided twice, and then invariably entered on all succeeding runs. The eighth cul de sac was avoided six times, entered once, avoided once, and then became fixed; in another case it was avoided for 28 trials, entered three times, avoided for five trials, and then became fixed. The continual avoidance of an error for a number of trials followed by invariable entrance can not be due to chance. Chance may account for the first entrance but the *sudden fixation* of the habit remains inexplicable. This type of behavior may be readily explained by our hypothesis. This alley is so related to the previous sections of the maze that the turning habits necessitated by the latter dispose the animal to avoid it. But these determining habits become altered with successive runs. The avoiding disposition becomes weakened and finally supplanted by the opposite attitude. The alley is thus regularly avoided for a while; there is indecision and alternation for a short period; and this behavior is followed by sudden fixation and invariable entrance. The fixation of this error is not due to repeated entrances. In a sense this error was engrained in the animal's organization before it was entered, because the disposition is the outcome of the entire maze[4] habit developed up to that time.

CONCLUSIONS

The temporal order in which the various cul de sacs are eliminated is roughly correlated sometimes with their spatial order in reference to the food box and sometimes with their order of proximity to the point of entrance.

The temporal order of mastery of the cul de sacs is invariably correlated with their order representing the increasing number of errors made in each. The ease or rapidity of mastery of any cul de sac is thus inversely related to its degree of attractiveness as measured in terms of number of entrances. The problem as to the order of elimination of the cul de sacs must be explained in large part in terms of the distribution of errors.

The factors influencing the distribution of entrances among the cul de sacs are the tendency to return, the character of the motives actuating the animal, and peculiarities of the cul de sacs.

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[4] This hypothesis is closely related to Peterson's conception developed in his recent article, Completeness of Response as an Explanation Principle in Learning, Psych. Rev., **23**, 153-162.

The amount of returning will vary with the animal, the maze, the stage of mastery, and the section of the maze.

The character of the motives will shift within a run as progress is made from section to section, and from one stage of mastery to another.

The attractiveness of cul de sacs due to peculiarities of construction or position must in part be interpreted in terms of the animal's organization in reference to them. As a possible hypothesis, it is suggested that these disposing conditions of the organism are a function of the maze habit as developed up to that time. With this conception the individuals of a group may vary in their attitude toward a cul de sac and the attitude of any individual may change as the maze is being mastered.

MOVING AND STILL LIGHTS AS STIMULI IN A DISCRIMINATION EXPERIMENT WITH WHITE RATS

CORA D. REEVES

The work here reported was done in the spring of 1912 under the direction of Prof. J. B. Watson, by whom the problem was suggested. As the work of others may be furthered I present briefly results compiled at the close of the experiment.

Apparatus.—The apparatus consisted of two crayon boxes, 9.3 x 10.5 x 16 cm., blackened inside and out, and each with a doorway cut in one end. To each, on the end opposite the opening, was attached a narrow, vertical support with a horizontal bar on the top of it. Suspended from this bar and immediately above the door was a miniature tungsten, 2 c.p. lamp, thus:

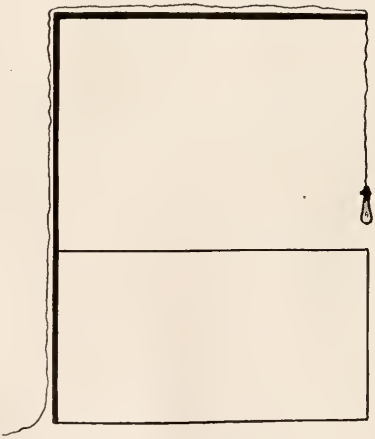

FIGURE 1.—Elevation of food-box

Rats tested.—The animals used were four male albino rats of the same litter. They had learned the maze but were not yet quite full grown.

Methods.—The boxes were placed upon the arc of a circle of 80 cm. radius near the end of a black-slate table of about a meter width. The following diagram will show conditions:

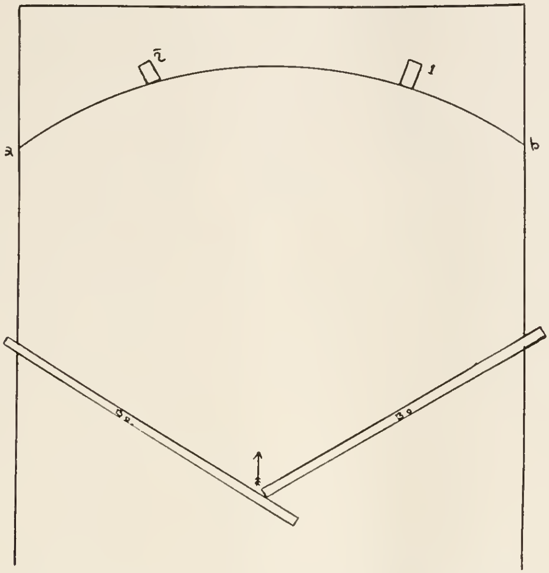

FIGURE 2.—Plan of apparatus. 1, 2. Food-box. Bo. Boards six inches wide which were placed on edge so as to pen off the area used in experimentation. a, b. Chalk line along which boxes were shifted. ←— indicates the position where the rat was placed and direction of the head.

Boards were used to close off the rest of the table. The experiment was carried on in a dark basement room and the black boxes were on the side of the room and of the table away from the light. Thus two dark objects against the dull background of the walls rested upon the slate table. Above these were the lights. The rats were kept in cages in the animal room and brought in a small wire cage to the room where the experiments were conducted. Before the rat was taken from the carrying cage a bit of food (bread soaked in milk) was placed in a dish in each box. A net was placed over the dish which was not to be in the food box for the rat being tested. The food and net were low in the dish and out of sight. This was to provide the same sensory stimuli in all particulars except the one to be discriminated. The light over the one box was started swinging by hand, moving through an arc of more than three inches and the light over the other box was left hanging still. The rat was dropped upon the table at the center of the circle (see fig. 2) or 80 cm. from each box. Care was taken to place the animal with head in the direction indicated by the arrow. A record of the time taken by each rat in reaching the box, and as to whether the choice was right or left hand, was made. The boxes were interchanged by chance. They were placed along the arc of circle at all points and all distances apart. The same box always had the light swinging. When the box had been reached and entered the rat was allowed to feed if correct choice had been made, and was then picked up and returned for another test. Two rats, A and B, were fed at the box with the still light; C and D at the one with the swinging light. The first days, ten trials were made each day for each rat; then twenty trials daily for the seven weeks the experiment continued.

Preliminary work.—The rats were put on the table and the time taken for them to reach a single box without light for 10 trials each. During these preliminary tests no food was placed in the boxes. The average time per trial was 32 seconds the first day. The second day A went to the box ten times, but B, C and D went to the box three, five, and five times respectively, then quit running about before reaching the empty box. The next two days food was put in the box; the average for the four was 9 seconds the first day, and 4 seconds the second day.

The following two days the two boxes were placed one with food and one without food. The average time for the rats to reach the box was 5.5 seconds for the first day, and 3.1 seconds the second day.

The following day the light was put above the food box and not made to swing. The rats A, B, and D behaved as on days when the light had not been there, at least, any hesitation if present was not sufficient to change materially the average time. The rat C, however, after two trials took a longer time each trial, looking at the light before starting and then refused to move when placed on the table.

The next day the light was started swinging over the one box while left still over the other. The conditions of the experiment had thus gradually been reached. The average time per trial for A, B, and D on this day was 1.7 seconds, for C 4 seconds.

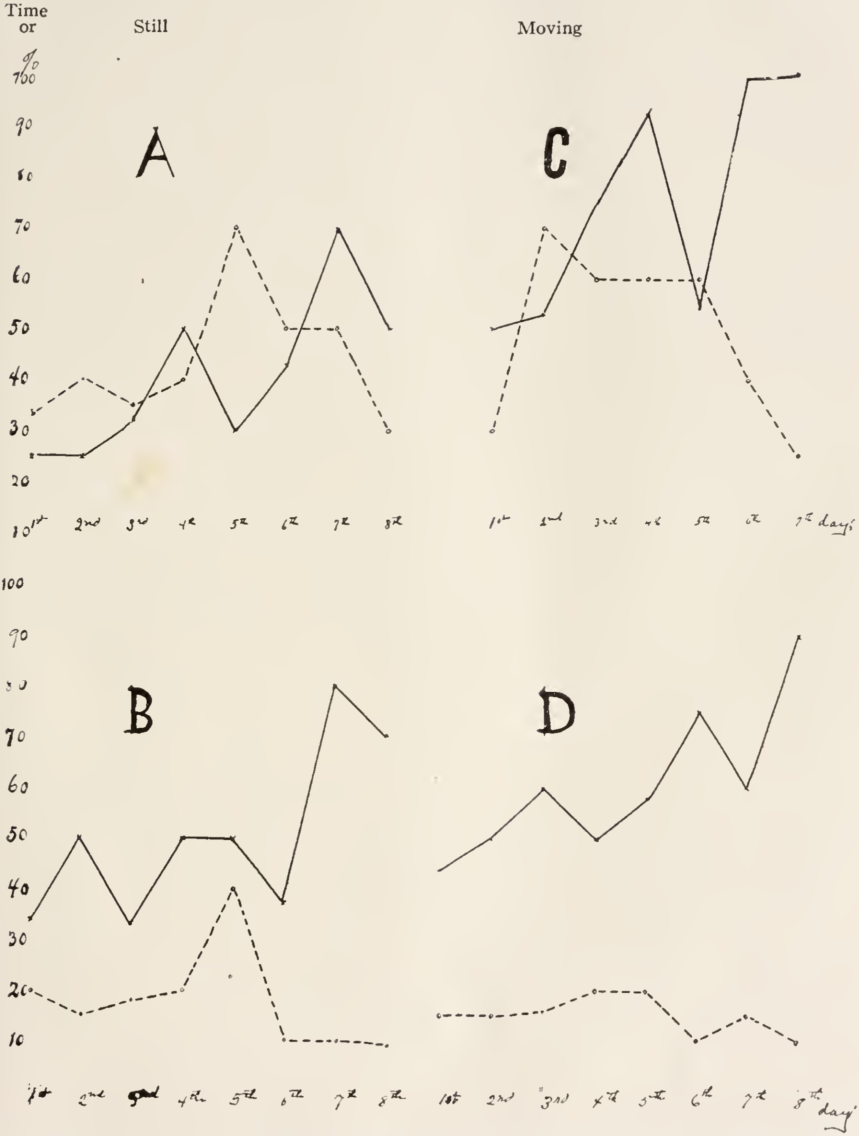

FIGURE 3.—Curves showing first responses of four white rats to stationary and moving lights. ———Per cent of correct choices for each successive ten trials. - - - - - - Average time in tenths of seconds.

The experiment.—Both A and B formed a rather persistent habit of going to the left hand box so that the first day's records of per cent of food choices have no significance. The days following, this habit was weakening and the correct choices increased. The preceding curves, fig. 3, show that A was slow in response as was also C, while B and D were habitually quicker in response. The curves show also that there was learning where the rats went to the moving stimulus, but with the others less high percentages of correct choice were made. Some tendency to decrease the average time for the day appeared.

On the eighth day, after two days of perfect record, the rat C was terrorized by a stranger with a dog entering the laboratory while this rat was on the table. An attempt to get again two days' perfect records caused the work to be prolonged for two months. After about two weeks (160 trials for each rat) the number of trials per day was increased to 20. There was an immediate increase in the average time per trial as shown by the following curve, fig. 4, which is made up from the time records of the four averaged for successive trials. The later trials for each day were slower. Evidently though only small portions of food were allowed each time the hunger stimulus was lessened after a few successful trials.

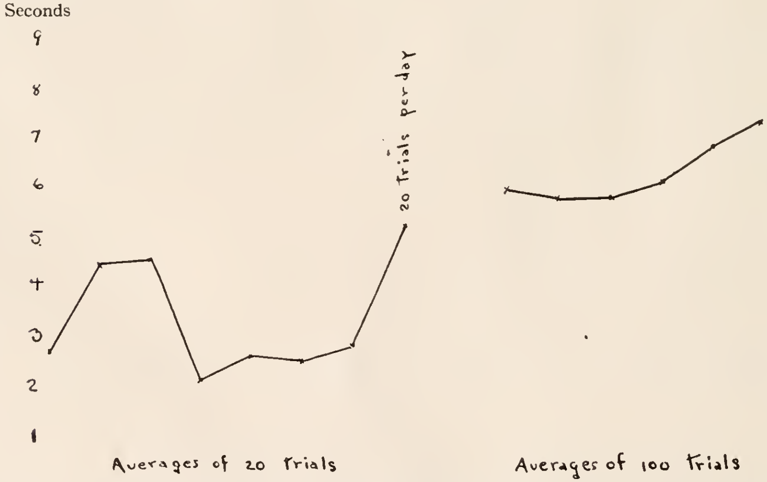

FIGURE 4.—Curve showing time in seconds for response to stimulus for four white rats while discriminating between still and moving lights during successive trials.

The first part of the curve is made by averaging together the averages of the successive 20 trials of each of the four rats; the last part the averages are for 100 consecutive trials.

The increase of time toward the end of the experiment is not easily accounted for. The age of the rats may be one factor. They, however, were not old but were then only full grown. The weather was warmer, and temperature and humidity may be other factors. The rats A and C were from the first (shown in fig 3) until the last days slower than B and D. For C the time average for the last 80 trials was 30 seconds. There is, then, no correlation between accuracy and speed of response. The rat A was the only one that toward the close of the experiment showed a reduction of the average time. Reference to the table which follows will show that the per cent of correct choices for this rat increases remarkably with the last 100 trials.

Table Showing Average Per Cent of Correct Choices in Discrimination of Stationary and Swinging Lights

	1st	2nd	3rd	4th	5th	6th	7th
Food at stationary lights:	100	100	100	100	100	100	100
Rat A	40	40	61	57	69	69	90
Rat B	57.5	52	53	64	58	63	78
Average	48.2	486	57	60	63.5	66	84
Food at swinging light:							
Rat C	76.5	66	68	71	76	86	86
Rat D	55	68	58	68	68	77	87
Average	65.7	67	63	68.5	72.5	81	86
Averages	57	56.5	60	65	68	71	85

The slowness and difficulty of establishing this discrimination is apparent from the table.

The error curves (fig. 5 on page 166) show the same slow process of learning to discriminate and further emphasize the tendency of the rats to go to the moving rather than the still light. The use of only four individuals makes the results less certain than would be the case had a larger number been used.

The records of rat A have frequent notes, as "Watching, moving back and forth, swinging or nodding while advancing."

This diagram of a path taken by A (fig. 6) shows a frequent sort of behavior for this individual, which was being fed at the still light. The starts toward the moving light were frequent and were followed by a pause and a run toward the still light. The swaying or nodding motion, rhythmic with the light, was

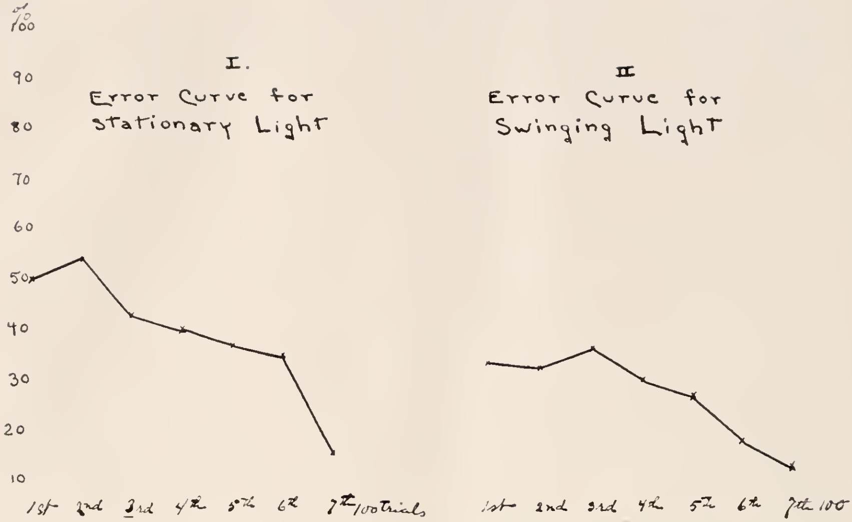

FIGURE 5.—I. Curve of error for rats A and B, fed at the stationary lights. II. Curve of error for rats C and D, fed at the moving lights. These show the average per cent of errors for each 100 trials.

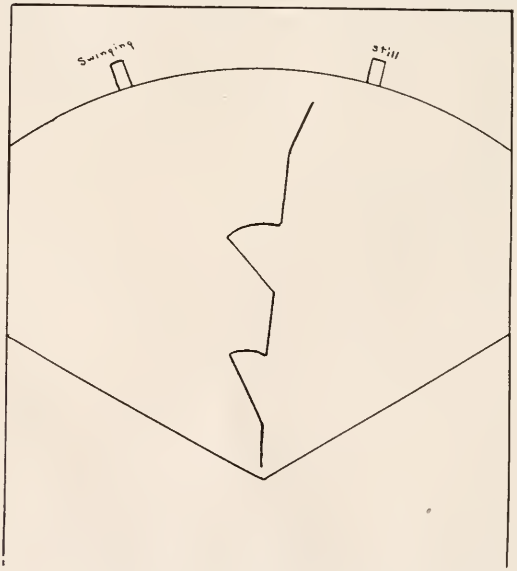

FIGURE 6.—Path taken by rat A in reaching the stationary light.

observed in rats A, C and D. While C and D started toward the still light at times, I have no records of paths of repeated starts and halts with change of direction as in the case of A.

Testing results.—To determine whether some clue given by the experimenter might not be the ground upon which the rats discriminated, Dr. Karl S. Lashley kindly tested the rats in my absence. There was an average of 80% of correct choices. In order to test further the significance of the results the rats which had been trained to go to the still light were placed as usual but with both lights still. They went equally to either box. A strange reaction occurred, for upon coming to the doorway of the box whose lamp had been swinging, when the vibrisse lightly touched the edges, rat A stopped, squealed, turned back and went over to the box which had had the still light. Apparently some sensation from contact dominated his reaction. The same halt at the doorway occurred when the rat C was presented with both lights swinging and he went to the box which had had the still light. One day when the rats trained to go to a swinging light were presented with both lights swinging in the middle of the day's series, the rat C for the four tests given, went to the box where accustomed to feed, but when the lamp which had been stationary was set swinging, while the light previously made to swing was still, this rat went to the box with the swinging light. D, when both lights were swinging, went to either box. The per cent of choices of the food box changed for this rat from 94 under standard conditions to 40 when both lamps were in motion. In other words, they went freely to the box which they had consistently avoided when the light stimuli were reversed. This fact together with the fact of the halt upon touching with the vibrisse the wrong box seemed conclusive evidence that the lights and not some other factor had been the effective one in making the choice when at a distance. After this halt at the doorway I noted that the small roughnesses of the edges of the doorway made by the saw were, of course, not exactly alike. I suspected that by chance or from attraction of the swinging lamp the rat C went to that box often and was then able to track himself but the evidence seems conclusive that the moving stimulus came to be the stimulus depended upon in reaching the box and food.

Discussion of results.—The large number of trials (700) necessary to establish this discrimination seems to indicate how small a part the visual stimulus, has in the daily life of a rat. Had it not been for the records of the first week and especially of rat C (fig. 3) and the lack of any adequate explanation other than "learning to discriminate" which would account for the improvement both in choice and in time, the conclusions (after each had had 200 trials) would have been that rats cannot discriminate a moving and still light. (See table.) The rats came in time to select the food box more accurately. In the fact that the rats halted at the doorway of the boxes where they had not been receiving food is an indication that they used other criteria than the lights when they reached the food box. They were, however, not able to select the right box when the condition of movement of the lamps was changed. It seems possible that some laboratory failures to find that animals possess as acute sensory mechanisms as have been popularly ascribed to them may be from the fact that the problem presented was not fitted to the animals tested. This incident will illustrate. At the close of this series of experiments an old rat which had been handled continually for some months was running about the room when the writer chanced to be winding up a piece of cord. As the end of the cord was drawn along the floor the rat followed, patted the end, for some eighteen inches, as a kitten would. This rat was tested several times with a cord but would never repeat the behavior. The rat became familiar with a new situation quickly but the stimulation afforded by a moving object could not be doubted. The effectiveness of movement in controlling reactions is shown in the difference in the curves (fig. 5) and in the path of the rat as shown in fig. 6. The lengthened average time when 20 trials per day were used instead of 10 confirms the evidence already presented that a large number of daily repetitions is not the most advantageous method of establishing a given discrimination.

CONCLUSIONS

1. Rats can and do discriminate a stationary from a moving light.

2. Rats show some tendency to approach a moving rather than a stationary light.

A NOTE ON THE INTERFERENCE OF VISUAL HABITS IN THE WHITE RAT

BINNIE D. PEARCE

From the Psychological Laboratory of the University of Texas

INTRODUCTION

The following experiments were performed at the University of Texas under the supervision of Professor W. S. Hunter,, from January to June, 1916. This paper should be considered as a continuation of researches made by him and should be read in connection with his paper on "The Interference of Auditory Habits in the White Rat."[1] The purpose of the present tests was to obtain data showing the strength of habit in the white rat by measuring the effect of a habit previously acquired upon the formation of a new habit of opposite character. The stimuli in each case were lights. The results appear to reinforce the conclusions reached by Dr. Hunter, viz., that a habit acquired by training does persist in the new work and may interfere tremendously with the formation of a dissimilar habit. My detailed conclusions will be presented at the close of the paper.

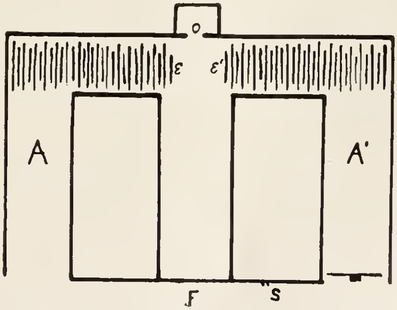

FIGURE 1.—Ground plan of the apparatus

The apparatus used was a T-shaped discrimination box and is shown in fig. 1. A mazda light was placed in a small box behind the main apparatus. Between the boxes was an aperture, O, covered with a piece of clear glass and a variable number of sheets of typewriter paper (Post Office bond). These variations and the c.ps. employed will be given below. The light was controlled with a switch at S. The rat was expected to react to the presence or absence of light by turning to the left or the right as the conditions of the experiment required and as will be detailed later. When the reaction to the stimulus was correct, the animal escaped through an open alley (A) to food at F; when incorrect, an electric shock was given by means of the wires marked E and E′ and a free exit was blocked by means of a movable end-stop, placed in the alley A′. At each trial the rat was introduced directly into the discrimination box through an opening at F and the stimulus was presented immediately. Punishment and reward was used throughout the test. The following series of presentations were used, 10 trials daily:

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[1] *Jour. Animal Behav.*, 1917, 7, 49-65

l l r l r r l r l r
r l l r r r l l r l
r r l r l l r l l r
l r r l r r l r l l

EXPERIMENTAL RESULTS

I

The present experiment was begun with four untrained rats (adults). Later four new untrained rats were added. Of these one (No. 10) was 42 days old; one (No. 13), 37; and two (Nos. 14 and 15) 68 days old. Unless otherwise stated the results given are for all eight rats.

On each of 3 consecutive days the animals were allowed to make 5 preliminary runs in the box, the object being to acquaint them with the apparatus and to accustom them to receiving their food at F. These trials were given without light stimulus, punishment or end-stops, save that the latter were used where necessary to prevent the appearance of position habits.

In the regular test, habit No. 1, a correct response required the rat to turn through the right hand passage when light was present and through the left hand passage when the light was absent. The light used in this first test was a mazda 32 c.p., shaded by one thickness of ordinary writing paper as mentioned above.

Table 1 shows the number of trials required by the rats in establishing the association. The standard of learning was as follows: Each of the last four series of 10 trials must show at least 8 correct reactions, but the average percentage of correct reactions for the four series must not be less than 87½%. The trials in table 1 include all given each rat up to the 40 made at the standard percentage.

TABLE 1

LEARNING HABIT NO. 1

Rats	Trials
1	170
2	180
3	80
4	190
10	300
13	220
14	60
15	120

A comparison of table 1 with similar data obtained by Dr. Hunter in his experiments on the acquisition of auditory habits[2] is of value in showing a greater ease in the formation of visual habits by the white rat. My rats ranged between 60 and 300 trials with an average of 152. Dr. Hunter's rats,—from the same stock, working in the same apparatus on the same problem, but using sound as a stimulus,—ranged between 210 and 710 trials with an average of 423. This is a matter of great importance inasmuch as the explanation would appear to lie chiefly, if not wholly, in the different sensory channels involved. I call to mind no prior demonstration of this fact. Extended study, which would go far beyond this preliminary work, would undoubtedly reveal important differences in vision and hearing so far as the daily life of the rat is concerned.

As each rat learned the association, control series were introduced as follows:

1. No light used; no punishment. Reaction considered right if it fits the series.
2. An 8 c. p. mazda substituted for the standard light. Punishment used.

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[2] Op. cit., table 1.

The object of control 2 was to determine the similarity of the 8 and 32 c.p. stimuli in terms of response. A summary of the control tests is given in table 2. The chronological order of records has been preserved. The per cents represent correct responses in a given daily series of 10 trials. The low percentages made with control 1 indicate the rats' dependence upon the light as a determining stimulus. The high percentages made with control 2 indicate that the rats sensed the light and that it meant to turn to the right in order to secure food. The exceptions to this statement are shown in the table.

TABLE 2

CONTROLS USED WITH HABIT NO. 1

	Rats							
Control	1	2	3	4	10	13	14	15
Control 1......	50%	80%	40%	50%	60%	60%	50%	50%
Control 1......	..	60	..	..	..	..	..	..
Normal.......	90	100	90	100	90	100	90	90
Normal.......	..	..	..	..	..	..	90	..
Control 1......	50	..	60	50	20	50	40	70
Normal.......	100	..	90	90	60	100	90	90
Normal.......	..	..	..	..	90	..	..	..
Control 2......	50	90	70	80	80	100	70	100
Control 2......	..	80	..	..	..	..	..	..
Normal.......	60	100	90	90	90	100	70	100
Normal.......	100	..	..	..	..	..	..	..
Control 2......	50	60	70	70	70	90	40	80

II

Training on the second habit was instituted in the case of each rat as soon as the results of the first test had been analysed by controls as shown above. The second habit furnished a problem the opposite of habit No. 1. Its purpose was to train the rats to associate turning to the *left* with the presence of light and to the *right* for the absence of light. The 8 c.p. light of the control tests was the stimulus here. At first it was shaded by three thicknesses of the writing paper. But when rat No. 3, the first rat tested on habit 2, persisted in reacting to this stimulus as he did to the absence of light, I removed one thickness. The purpose was to secure a light which would be treated the same as the standard light and yet which should be as different in intensity as possible from the standard.[3] The situation is summarized in table 3. The first reactions of the rat to the twice-shaded, 8 c.p. light were made as though this light were the standard light of habit 1. (Reactions to the normal stimulus should give at least 80% correct. Reactions to darkness would all be made to the left and so would give 50% correct. Since the new series, habit 2, was the reverse of the "normal" series, when the rat treated the stimulus as though it were the normal standard light, he should make not more than 20% correct.) I now knew that the once-shaded 32 c.p. and the twice-shaded 8 c.p. would initiate the same responses. Furthermore, there was reason to assume, both from the behavior just cited and from the work of other investigators, that the lights were dissimilar enough in intensity (one being almost equivalent to darkness) that they could be readily discriminated by a rat when tested in the conventional discrimination box.

TABLE 3

Test	Correct in 10
Normal (32 c.p., once shaded)	9
New series (8 c.p., thrice shaded)	5
" " " " "	3
" " " " "	5
" " " " "	5
" " " " "	5
" " " " "	4
New series (8 c.p., twice shaded)	1

In this second test every effort was made to keep the conditions identical with the first test save in the matter of light stimulus and direction of turning. The results are very striking. In the first test, the least number of trials given any rat was 60 and the greatest 300. In the second test, one rat learned in 420 trials. The other seven rats never completely learned the association,—the trials given were 680, 760, 850, 1080, 1080, 1090, 1090, and 1160. At the close of the work these rats were improving so, that it seems probable that they would have mastered the problem had the training been more extended. The results of this test are summarized in table 3. The length of the training periods here as opposed to the learning periods with habit No. 1

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[3] It would be of value and interest to have animals form habit No. 2 with the same stimulus used in habit No. 1. My choice of stimulus for the second habit was guided by a desire to secure a procedure similar to that followed by Dr. Hunter.

TABLE 4

Correct Reactions in Each Succeeding 50. Habit No. 2

	Rats							
Trials	1	2	3	4	10	13	14	15
50	13	5	23	13	14	9	21	12
100	18	16	17	7	11	13	17	16
150	16	20	10	13	12	12	15	27
200	13	20	18	17	16	14	20	17
250	20	17	27	18	17	9	21	30
300	12	15	23	24	18	13	21	34
350	14	19	25	14	17	15	31	31
400	10	20	26	18	18	16	32	43
450	15	20	25	16	23	26	32	15 of 20
500	17	18	18	19	25	25	30	
550	19	19	25	21	28	27	41	
600	15	10	22	23	26	29	41	
650	17	16	22	26	21	33	34	
700	17	21	24	25	22	27	27 of 30	
750	22	17	28	31	27	26		
800	29	26	32	28	3	26		
850	22	24	29	30	of	24		
900	22	32	30	28	10			
950	25	27	30	41				
1000	27	35	32	33				
1050	30	41	27	33				
1100	26	20	29	24				
1150	of	of	31	of				
1160	40	30	7	40				
			of					
			10					

are not to be explained by variations in age (which were too small) or in experimental conditions. The essential factor is the interference of habit No. 1 with the formation of habit No. 2.

The following is a brief examination of representative data secured on habit No. 2. Rat No. 3 had acquired the first habit with great facility after 80 trials. After 1160 trials on the second association he was making only 31 correct reactions out of a possible 50. This rat when set upon the new problem was in perfect condition and had shown no tendency to untoward timidity or the formation of position habits. When presented with the second problem, he at first reacted to the stimuli (8-c.p. light for turning to left; darkness for turning right) as if they had been the former stimuli (32-c.p. light for turning right and darkness for turning left). Upon punishment he immediately set up position habits from which he could be forced only with difficulty and into which he fell again and again. Several times he slowly approached the standard of learning; but when he seemed about to attain it, the position habit would again appear. This conduct was characteristic of all rats, save that rat No. 15 did master the problem. This error-behavior need not be regarded in its entirety as an interference phenomenon, because it occurs in the course of all difficult problems. However, it is to be remembered that the present discrimination of light from darkness is not a difficult problem. Table 5 gives sample records illustrating the above factual statements concerning position habits.

TABLE 5

Diary Records Showing Fluctuating Behavior in Learning Habit No. 2

	Rat No. 4
April 27	8
28	9
29	5
30	5
May 1	5
2	6
15-22	8, 8, 8, 9, 6, 6, 7, 5
	Rat No. 14
May 16-28	8, 9, 8, 8, 8, 7, 7, 6, 10, 9, 9, 7, 4

III

Rat. No 15 was the only one who mastered habit No. 2. This animal was 68 days old when first tested. He acquired habit No. 1 in 120 trials (tables 1 and 2), was put through the controls and immediately started upon habit No. 2. This was mastered in 420 trials (table 4). A control similar to control 1, used in analyzing habit No. 1, was instituted and proved that No. 15 was reacting to the stimulus (light) presented.

A third problem was then set No. 15,—a test in retention. The rat was put back on habit No. 1, the operator again using as stimulus the 32-c.p. light (shaded as before in habit 1). The rat was tested for 15 days, 10 trials daily. Habit No. 2 persisted and interfered with the training on habit No. 1 so that the percentage of correct reactions never exceeded 50 for any 10 trials. By the close of the 150 trials a position habit of always going to the left had fixed itself upon the rat with such tenacity that tests were discontinued.

I have plotted three curves, fig. 2, which present graphically the learning processes detailed above. The curves are constructed as follows: The total number of trials given a rat prior to the 40 made at the standard is divided into 10 parts. The percentage of correct reactions in each one-tenth is then computed and an average for all rats taken. The resulting curve shows the progress of error elimination independently of the absolute number of trials and is thus representative throughout its length. N indicates the records during the 40 trials made at the standard percentage.

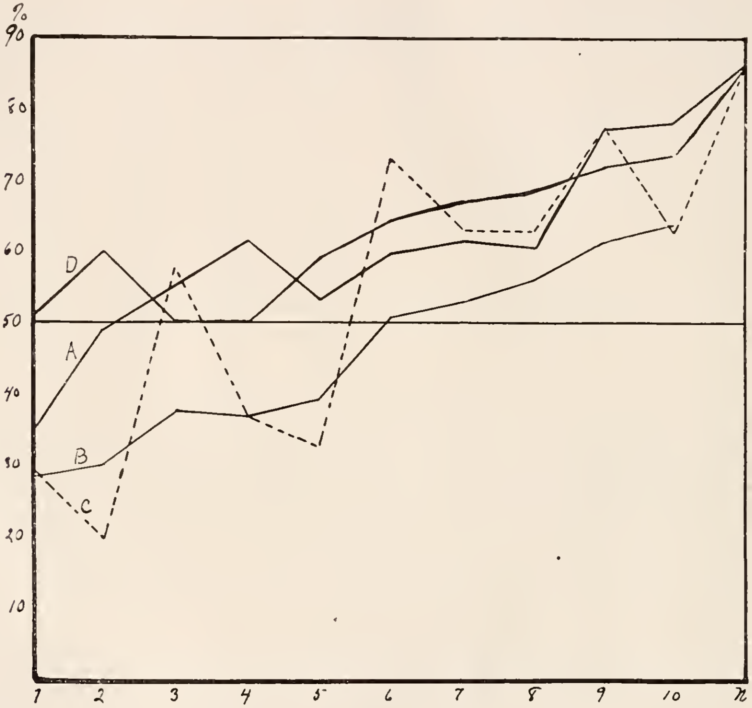

FIGURE 2.—Curves of learning. A—record for all rats on habit No. 1; B—record for all rats but No. 15 on habit No. 2; C—record for rat No. 15 on habit No. 2; D—record for Hunter's rats on learning a first habit in audition.

Curve A shows the succeeding average percentages of correct reactions for all the rats during the formation of habit 1. It is essentially the same as curve D. Curve D is taken from Dr. Hunter's "Auditory Interference" study, table 7. It is a normal curve of four rats on sound. The practical identity of the two curves is interesting in view of the different absolute lengths of time involved in the formation of the two types of habits.

Curve B presents the results for habit 2 for all rats save No. 15. It is a curve of progress and not of completed learning. Curve C is the record for rat 15 on habit 2. The curve is irregular in its first part. Curves A, B, and C indicate that so far as rate of error elimination is concerned, habit interference has been most prominent in the first six-tenths of the curves. Dr. Hunter's results also indicated that the six-tenths point was a turning point in the relearning process. The situation may be but a coincidence, however.

CONCLUSIONS

1. A simple visual habit of the type here studied will interfere tremendously with the formation of another visual habit of opposite kind. This interference may practically prevent the formation of the second habit.

2. A comparison of our data and Dr. Hunter's indicates that the white rat learns visual habits much more readily than similar auditory habits.

MODIFIABILITY OF THE PREFERENTIAL USE OF THE HANDS IN THE RHESUS MONKEY

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Observations on handedness in monkeys and apes has not, in general, given evidence for the predominant use of either hand which might be ascribed to heredity and in this respect has not provided phylogenetic support for the view that handedness in man is instinctive. Pfungst ('12) reported that in observations on over sixty individuals of different genera the instances of predominant use of either hand could almost always be traced to training or to previous trauma. He has not, however, reported the details of his work. Franz ('13) found that of six monkeys (Macacus rhesus) two were ambidextrous, three used the left hand more frequently than the right, and one was probably right-handed, but doubtful because of the small number of observations which could be made. Lashley and Watson ('13), studying a very young monkey, were unable to demonstrate the predominant use of either hand. Yerkes ('16) made tests upon seven apes, four of which were found to be predominantly left-handed, one right-handed, and two probably ambidextrous.

Except in the work of Franz not enough observations of any one animal have been reported to demonstrate such a persistent predominant use of one hand in a variety of activities as is necessary for a comparison of the condition in the animal with handedness in man. During the past summer Dr. Franz placed two young male rhesus monkeys at my disposal, suggesting a continuation of the work upon the preferential use of the hands with a view to the permanent modification of the normal condition by training.[1]

Observations were made first upon the preferential use of the hands in a number of different situations to test the effects of the immediate environment upon the reactions. An attempt was then made to alter the proportionate use of the hands. As the animals were to be used in other experiments the time available for this work was limited and it was not possible to undertake a permanent modification of their activity: a successful suppression of such an instinct would perhaps require a year or more. Since the complete alteration of an instinctive preference would necessitate the production of an altered predominance in the use of the hands under conditions in which training had not been given, a question of primary importance for the problem is the possibility of transfer of training from one situation to another, and the time available was sufficient for a limited study of this. The observations upon the animals' behavior in different situations formed a basis for a test of such transfer, requiring that the training be carried out in only a part of the situations.

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[1] These animals were purchased with a fund granted by the Carnegie Institution of Washington to which acknowledgment is here made.

The observations were made upon the animals, in part while they were in the cages described earlier by Franz ('13), in part while they were fastened by a strap one meter in length to a swivel snap in the floor of the room where the monkeys were kept. In the tests upon the use of the hands in taking food the following seven conditions were used.

Animal fastened to the floor with the strap.—

1. Picking up food from the floor. The food was dropped as nearly as possible in front of the animals and within easy reaching distance.

2. Taking food from the experimenter's right hand. The food was held directly in front of the animal and about 10 inches from him, so that he could reach it equally well with either hand.

3. Taking food from the experimenter's left hand. The conditions were otherwise as in situation 2.

Animal in the cage.—

4. Picking up food from the floor of the cage.

5. Taking food from the experimenter's right hand. His fingers, holding the food, were thrust through the coarse wire netting of the front of the cage so that the monkeys did not need to reach out of the cage to get the food.

6. Taking food from the experimenter's left hand. Conditions were otherwise as in 5.

7. Taking food from a small table placed in front of the cage and about six inches above its floor. The animals had to reach through the meshes of the netting to get the food in this situation.

Except when holding out food in his hands the experimenter remained at a distance of about four feet from the animals during the observations. The animals were rather wild at first and about two weeks were spent in handling them and accustoming them to the experimenter before the observations on the preferential use of the hands were begun. The two were markedly different in temperament. The smaller (No. 1) was gentle and almost fearless, rarely hesitating to take food from the experimenter's hands. The larger (No. 2), on the contrary, was exceedingly wild and fierce, constantly trying to break his strap, when out of the cage, and striking and biting at the experimenter when food was offered.

The tests were made at irregular times but several of the situations were included in each day's observations in order to control temporal variations in the use of the hands. With few exceptions the results of observations on different days are in agreement so that we may be sure that they are not due to a temporary injury of one or other hand.

PREFERENTIAL USE OF THE HANDS WITHOUT TRAINING

The number of times which the right and left hands were used by the two animals in each of the seven situations is given in table 1. There is a considerable amount of variation, depending upon the different environments in which the animals were placed, but the behavior of each animal is fairly characteristic throughout. No. 2 was obviously right-handed, using the right hand almost four times as frequently as the left. No. 1 showed a less marked preference for the use of either hand and a much greater adaptability to the different situations. In picking up food from the floor of the cage, where he was least influenced by the presence of the experimenter, he used his left hand in over 90% of the cases observed; a fact which indicates a decided left-handedness. Where food was offered in the experimenter's hands, however, he reached for it in 81% of the trials with the hand homologous to that used by the experimenter. Under like conditions No. 2 was not influenced by the hands of the experimenter, using the homologous hand in only 55% of the cases.

TABLE 1

Preferential Use of the Hands Under Different Environmental Conditions in Two Rhesus Monkeys

Conditions of Test	Monkey No. 1				Monkey No. 2			
	Number of cases in which each hand was used		Per cent of cases in which each hand was used		Number of cases in which each hand was used		Percent of cases in which each andh was used	
Hand used	R	L	R	L	R	L	R	L
Monkey in cage, taking food from—								
a—experimenter's right hand	146	102	59.7	40.3	264	70	79.1	20.9
b—experimenter's left hand	46	155	22.0	78.0	174	42	80.5	19.5
c—floor of cage	23	243	8.6	91.4	120	57	67.2	32.8
d—table before cage	59	41	59.0	41.0	200	4	98.0	2.0
Monkey on floor outside of cage, taking food from—								
e—experimenter's right hand	386	47	89.1	10.9	158	8	95.2	4.8
f—experimenter's left hand	3	164	1.7	98.3	60	40	60.0	40.0
g—floor of room	133	192	40.9	59.1	30	46	39.4	60.6
All trials	796	944	45.7	54.3	1006	267	79.4	20.6

A like predominance in the use of the hands was found in reactions of defense. With the monkeys fastened in the middle of the floor the experimenter touched them lightly on top of the head with the tips of the fingers of his right hand. The monkeys reacted to this by striking at his hand or by attempting to grasp and bite it. The number of times in which each of the two hands was used in warding off the touch is shown in table 2. Number 2 was as markedly right-handed in this as in his food-taking reactions. No. 1 again appeared to be left-handed, but only to a slight extent.

The predominant use of the hands seemed associated with the positions assumed by the monkeys when kept alone in different cages. They ordinarily sat in one of the rear corners of the cage and the corner chosen was usually that which gave the greatest freedom to the hand most frequently used. Thus No. 1 sat with his right side near the side of the cage, leaving his left arm free, and No. 2 kept his right arm and side away from the side of the cage. Interchanging the monkeys in their cages did not seem to interfere with this custom, which seems therefore independent of the relation of the cages to other objects.

Marked variations in the use of the hands from day to day were noted. Not more than 25 trials in any one situation were given on a single day and in the majority of cases one or the other hand was used exclusively in each series of trials unless some disturbing element, such as the alternate use of the experimenter's hands, intervened.

TABLE 2

The Preferential Use of the Hands in Defence from Attack by the Experimenter

	Hand used to ward off blow		
	Right	Left	Both
Monkey No. 1:			
Number of cases	70	122	13
Per cent of cases	34.2	59.5	6.3
Monkey No. 2:			
Number of cases	129	33	6
Per cent of cases	76.8	19.7	3.5

TRANSFER OF THE EFFECTS OF TRAINING

When a sufficient number of observations had been obtained to make the relative use of the hands in each situation fairly certain, training for the exclusive use of one hand was begun. An attempt was made to force both of the animals, when leashed to the floor of the room, to use only the left hand in taking food from the experimenter's right hand. The method of training was to withhold the food and to grasp or strike at the monkey's right hand whenever he extended it to take the food. No. 2 did not take kindly to this training. He would snatch at the food with his right hand, getting it as often as not, and when punished would refuse to reach again. After about 100 trials he could no longer be induced to make any attempt to get the food and further training had to be abandoned.

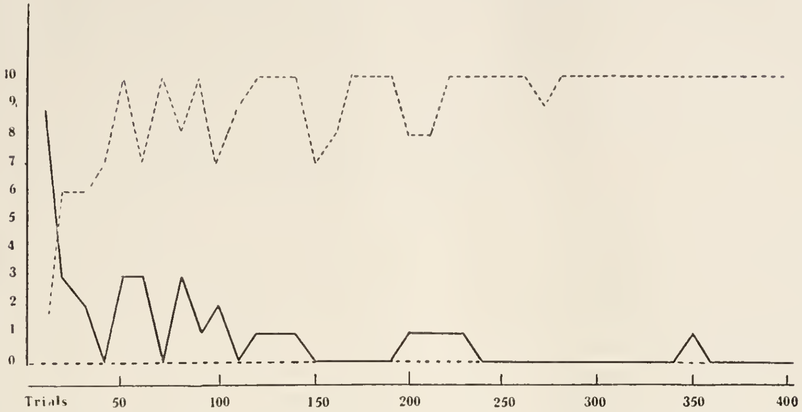

FIGURE 1.—The course of modification of the use of the right hand by training in the case of monkey No. 1. The ordinates represent the number of times that the right hand was used in each successive ten trials, the abscissae, the number of trials grouped by tens. ———— first period of training. - - - - - - - - - - - - second period.

No. 1 learned to inhibit the use of his right hand very quickly. After nine successive failures to get the food with his right hand he began to use his left predominantly and only 34 failures to get the food were required to abolish completely the use of the right hand in this one situation. The form of the learning curve is shown in fig. 1. After the first hundred trials the left hand was used in all but 2% of his efforts to get the food.

When the habit seemed firmly established (after 500 trials) the preferential use of the hands in the remaining six situations was tested again. The data obtained are given in table 3. In the three situations outside of the cage the training resulted in a decrease in the use of the right hand. This is not very certain where the animal took food from the experimenter's left hand, since there was little room for improvement to begin with, but it is unmistakable where food was picked up from the floor. In contrast to this the training seems to have had little effect in modifying the use of the hands when the animal was in the cage, except in the last case, that of taking food from the table. The change here from 59.0 to 4.4% in the use of the right hand is significant.

TABLE 3

The Effect of Training in the Use of the Left Hand in One Situation Upon the Reactions in Other Situations. Monkey No. 1

Conditions of Test	Before training				After training			
	Number of cases in which each hand was used		Per cent of cases in which each hand was used		Number of cases in which each hand was used		Per cent of cases in which each hand was used	
Hand used....................	R	L	R	L	R	L	R	L
Animal on floor outside of cage; taking food from—								
a—experimenter's right hand ... (Training in this situation)	386	47	89.1	10.9	0	180	0.0	100.0
b—experimenter's left hand.....	3	164	1.7	98.3	0	95	0.0	100.0
c—floor of room................	133	192	40.9	59.1	11	141	7.2	92.8
Animal in cage; taking food rom—								
d—experimenter's right hand ...	146	102	59.7	40.3	45	35	56.2	43.8
e—experimenter's left hand.....	46	155	22.0	78.0	14	62	18.0	82.0
f—floor of cage................	23	243	8.6	91.4	14	59	19.0	81.0
g—table before cage............	59	41	59.0	41.0	5	98	4.4	95.6

At the end of these tests training for the exclusive use of the right hand was instituted. The situation and method were the same as in the preceding training, with the exception that food was now withheld from the animal's left hand. After a very few trials he began to use his right hand and a total of only 40 failures was required to bring about the exclusive use of the right hand. The course of learning is shown by the dotted line in fig. 1. Tests for transfer of this training could be made only for the situation of taking food from the experimenter's left hand. The transfer was evidently complete for this condition, the animal using his right hand in 49 out of 50 trials.

DISCUSSION

With clear evidence for a transfer of training in some situations and not in others, we must ask the reason for the selection. The one character in common to the situations in which transfer occurred and differentiating them from the others was the presence of the wire netting of the cage between the experimenter and the animal. When on the leash the monkey was directly exposed to attack and in taking food from the table in front of the cage he had to put his hands between the wires of the front of the cage and so expose them to attack. The stimuli from the presence of the wire netting between the monkey and the experimenter seem, then, to have formed the limiting condition for the transfer of training.

An attempt at a further analysis of the rôle of these stimuli in determining the transfer is hardly justified by our present knowledge. In their cages the animals frequently give more threatening reactions than when held by a leash, so it may be that a certain physiological tone or emotional reaction, common to a part of the situations, reinforced the habit and led to its transfer to all of them in which it was present. The transfer might also be looked upon as the result of an analysis of the situations in ideational terms, but this and the concept of physiological tone are, themselves, so badly in need of experimental analysis as to amount to nothing more than a restatement of the problem when applied as explanatory principles. We can say safely only that the habit of using the left hand was conditioned by a complex group of stimuli.

The ease with which the predominance in the use of the hands may be altered by training will make it very difficult to establish the existence of any hereditary predominance. We never know the complete history of an animal or can exclude the possibility of a severe trauma which might condition the use of one or the other hand. Only the observation of the predominant use of one hand in a wide variety of situations and in situations entirely new to the animal could furnish reliable evidence for an hereditary predominance.

The possibility that the use of the hands by human infants may be equally easily modified by training makes the existing data upon handedness in young children of very doubtful value. Mrs. Woolley ('10) believed that the predominant use of the left hand by the infant which she studied was the result of the carrying position,[2] but experimental evidence upon the acquirement of such habits by young children is lacking.

SUMMARY

1. The rhesus monkey, as has been shown by Franz, may be right or left-handed or may use the hands indifferently.
2. Immediate adaptation in the preferential use of the hands in different situations may appear.
3. Where there is no decided preference, the use of the hands may be modified very easily for a given situation by training.
4. There is a transfer of training to new situations, but these are selected on the basis of complex stimuli.

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[2] Max Meyer ('13) has criticized this interpretation upon inadequate grounds. He says concerning it, " If our ancestral inheritance could be so easily modified as Mrs. Woolley supposes, what an incentive this would be to enthusiastic educators! " Here he evidently overlooks the fact that the great mass of habits formed by infants and young children (the social inhibitions) are just such modifications of instinctive behavor and that the modification is a process both rapid and productive of enduring results.

DIURNAL ACTIVITY OF THE EARTHWORM

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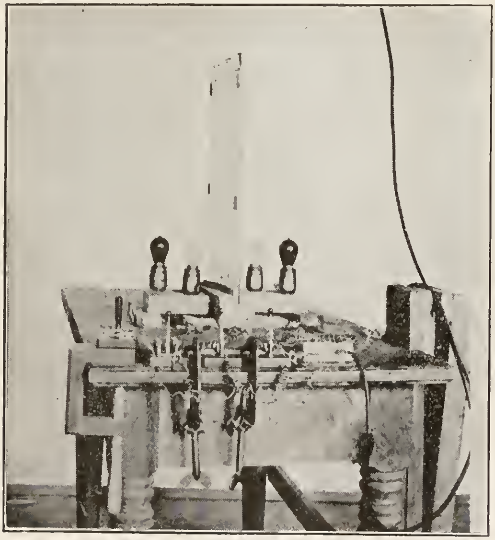
This note[1] records a series of observations made to determine whether the earthworm gives evidence of fixed periods of activity and of quiescence. Under the conditions of our observations, activity included (1) crawling movements either in or out of the artificial burrow, (2) feeding and the acquisition of food, and (3) the ejection of waste products from the body. Local contraction of segments was not regarded.

Apparatus.—Two parallel glass plates (12 in. x 20 in.), set 3-8 in. apart, were mounted in an upright position on a base 15 in. square covered at the lateral edges and filled in with



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[1] A summary of work done some time ago in the biological laboratory of Clark University, under the guidance of Professor C. F. Hodge. So far as the writer is aware, the work has not since been duplicated with this form. The author's thanks are due to Professor Bentley for suggestions in the preparation of the summary.

moist earth. Strips of black cloth were then tacked to a frame around the margin of the board, making a dark box to include the plates. Holes were cut in the cloth on either side for observation, a flap of cloth serving as a cover to the hole when not in use. Within were placed four 1-c.p. electric bulbs (two on either side of the glass) which were controlled by switches.

Large subjects of Lumbricus terrestris were used throughout the observations (four in the first series, and five in all the others). They were placed, one at a time, upon the surface above the plates and allowed to burrow into the soil beneath (between the plates), where their subsequent activity could be followed. The soil was kept moist by occasional sprinkling.

In preliminary observations, records were taken at 20-minute intervals, at various times of day and night throughout the period of one month. From data thus accumulated, the activity of the four subjects is summarized (in minutes) in table I, which indicates that the worms were active about one-third of the entire time with a fairly wide individual variation.

TABLE I

Subject	Total time observed	Total time active	Variations from average active time
I	18,060	7,740	2,324
II	18,070	6,000	584
III	16,200	3,840	1,576
IV	16,210	4,080	1,336
Averages	17,135	5,416	1,455

Records of the activity of five subjects were subsequently made on two different days (about a week apart), the observations being continuous for each of twenty-four hours. Table II displays the results for the two days (a and b), giving "active" times in minutes, by quarter-days.

Although moderate individual differences in amount of activity again appear, the average active time, when compared with the total time of observation (1,440 min. for the whole day) closely approximates that shown in table I. It is further to be noted that the period of greatest activity, with but two exceptions (I-a and III-b), falls within the hours 6-12 P. M.

TABLE II

Subject	Days	A. M.		P. M.		Total active times	Variations from ave. time (373)
		12-6	6-12	12-6	6-12		
I	a	80	24	30	**252**	386	13
	b	48	45	**207**	147	447	74
II	a	54	126	12	**134**	326	47
	b	72	48	42	**195**	357	16
III	a	54	12	03	**218**	287	92
	b	**177**	32	**140**	126	475	102
IV	a	60	54	18	**186**	318	55
	b	66	108	60	**134**	368	05
V	a	...	52	30	**270**	352	21
	b	54	102	120	**137**	413	40
Averages						372.9	46.5

TABLE III

Subject	Days	A. M.	P. M.		Total active times	Variations from ave. time (259)
		8-12	12-6	6-12		
I	a	40	54	**236**	330	71
	b	10	54	**120**	184	75
II	a	35	78	**274**	387	128
	b	24	65	**115**	204	55
III	a	30	36	**73**	139	120
	b	70	70	**145**	285	26
IV	a	18	69	**138**	225	34
	b	19	60	**165**	244	15
V	a	12	45	**294**	351	92
	b	60	50	**135**	245	14
Averages					259.4	63.0

In a similar manner, the activity of five other subjects on parts of two days (a and b) is shown in table III. In this series the period 12-8 A. M. was not included in the record.

Again the ratio of the average active time to the total time observed is, in this case, very close to that given in table II

TABLE IV

Subj.	Days	A. M.	P. M.		Total active times			Variations from average times (211, 364, 156)		
		8-12	12-6	6-12						
I	a	54	144	66	264			53		
	b	78	66	168		**312**			52	
	c	. .	11	126			137			19
II	a	. .	60	65	125			86		
	b	84	144	156		**384**			20	
	c	. .	48	132			180			24
III	a	60	138	72	270			59		
	b	104	140	174		**418**			54	
	c	. .	48	78			126			30
IV	a	72	84	48	204			07		
	b	78	110	162		**350**			14	
	c	. .	24	132			156			00
V	a	98	66	30	194			17		
	b	98	104	156		**358**			06	
	c	. .	42	138			180			24
Aves. .					211.4	364.4	155.8	44.2	29.2	19.4

(approximately 1:4), and again the period of greatest activity of the subjects is found to lie between the hours 6-12 P. M.

To determine the influence of food placed at the mouth of the burrow on the activity of the worms three series of observations were made and the results summarized in table IV. The letters under " Days " refer to the records of three successive days, before (a), while (b), and after (c) food was placed at the mouth of the burrow.

It appears from the above table that the presence of food at the mouth of the burrow tends to increase the activity of the worms, as indicated in the record of b. Activity is least upon the day (c) following its removal.

These observations lead us to conclude that (1) in spite of individual differences the total active time, when compared to the total time under observation, is fairly constant, that (2) the earthworm has definite active periods, confined, for the most part, to hours of the night, especially to the early hours of the night, and that (3) food has a decided effect upon activity.

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THE FEEDING OF NESTLING BIRDS*

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As a basis for the discussion which will follow I wish to inquire into the validity of field study as a method of developing our knowledge of bird-life. In a broad sense, by the term " field study " we mean the study of the living animal in its native habitat, under normal conditions; or under abnormal conditions which are known and determined.

It seems to me that it must be accepted as axiomatic that we have no other method of approach to certain problems of behavior. Even if this is true, however, it does not follow that the results obtained by such method are any the less subject to scrutiny and criticism. We must demand of the field zoologist the same accuracy of observation, the same careful exclusion of uncertainties, and the same rigid logic that we require of the worker in the laboratory. The observational and experimental methods are open to the one who will attempt to solve the problems of nature in the field. The laboratory worker relies upon the same methods.

I would contend, therefore, that the reliability of field studies stands in direct ratio to the scientific spirit of the investigator. The value of a report based upon field studies cannot be judged apart from the personal equation; and is this not true of every kind of investigation? Do we not require that research carried out in the laboratory be subject to verification? And is not the knowledge derived in the field by the process of observation or experimentation also open to verification?

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*Address of retiring president of the Wilson Ornithological Club at its third annual meeting, at Columbus, O., December 29, 1915.

The successful pursuit of scientific knowledge depends upon the investigator's ability to observe and interpret; which, in turn, is largely a matter of training. Whether the observer sees through the lens of a microscope, the field glass, or with the naked eye, matters little. He is just as liable to err by the one as by the other, unless he is trained to recognize the avenues of error. Various technical equipment may be called to the aid of the observer, but, fundamentally, credibility is determined by the student's capability and honesty.

A given method of study must be appropriately used, and its limitations recognized. The microscope is to enlarge an object which is too small for direct observation. The field glass, in effect, is to bring the object closer. Both are for the purpose of rendering vision more distinct. It seems, therefore, that the field glass is as legitimate an instrument for research as the microscope. Its usefulness, however, is in the field. The extent to which it may be applied is a detail. In the identification of birds its use may be legitimate when the species possesses marks by which the identification may be thus determined. When specific differentiation is based upon minor variations in dimensions, the field glass becomes inadequate, and it must be so recognized. On the other hand, is there not also a danger that the taxonomist may go too far with his millimeter rule in the differentiation of species and subspecies?

It may be admissible to again raise the question whether, in the long run, science is advanced by the excessive multiplication of named forms which are based upon such minute structural details that the methods at the disposal of the field student become inadequate.

The tendency toward species "splitting" under the technical term of " revision " does not seem to be waning, and its bearing upon the field zoologist is so pertinent that the mention here may not be out of place.

Those ornithologists who are interested in the subject from the practical, or economic standpoint are concerned chiefly with the various problems which grow out of the question of the food of different species. Usually, the end in view, from this standpoint, is to determine the relation of birds, and of any given species, to man and to other animals in which man is economically concerned. While all of this has also a scientific value, yet the horizon taken in from the viewpoint of pure science has a vastly wider field than that which is involved in an economic study.

Without attempting to scan the entire horizon we may at once select the limited field into which we now wish to inquire. One of the subjects which has received a relatively small amount of attention is concerning the behavior of birds, and its interpretation; and particularly the behavior of birds during the breeding period, about which there is so much to learn. It is true that within recent years much more attention is being given to this phase of ornithology; but notwithstanding a rapidly growing literature along this line, on many of the problems there is not yet sufficient knowledge to enable us to safely generalize.

While other causes may have played a part in the slow development of our knowledge of the behavior of birds, it seems not unlikely that it is to be attributed, at least in part, to some prejudice against the reliability of field observations.

There are some problems which may be checked by laboratory technic, and in such cases our knowledge cannot be complete until such a check is applied. But there are some questions, which from their nature, can only be studied in the field (with respect to many species, at least). For example, there are many matters of detail about the mating of the sexes, the building of the nest, and the care of the young, etc., which cannot well be examined in the laboratory.

So when we consider the question of the feeding of nestling birds it seems that our most important method of study, and perhaps the only method in some cases, is to watch the process in nature and record the observations.

I will now review, insofar as my study of the subject permits, the facts which have been ascertained concerning the manner in which young birds are fed.

A considerable number of birds, among which, of course, are the *Limicolae*, are precocious, and forage for themselves from the beginning. Smith's paper on the Spotted Sandpiper (1)[1] reported the feeding behavior of sandpiper chicks for as early a period as I know of.

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[1] Numbers in parenthesis refer to bibliography, and page citations will sometimes be given also.

In this instance the young, which hatched during the night, were under observation from daylight of the morning of hatching, and the parents were not observed to carry any food to the young. On the other hand the young left the nest within five or six hours to feed for themselves.

If we now direct our attention to those birds which feed their young for a period of time we find considerable range of behavior. As a preliminary analysis of the subject we may distinguish three modes of feeding the young, viz.;

(a) Where the young bird thrusts its bill, or entire head, into the mouth or throat of the parent; or where the parent regurgitates the food, in a more or less digested condition, upon the ground, to be picked up by the young bird.

(b) Where there is insertion of neither bill, but a peculiar intercrossing of bills to be described in detail further on.

(c) Where the parent inserts its bill into the mouth or throat of the young in the delivery of food.

We may consider these methods in order. Perhaps the best example of the first method is furnished by the Pelican. From Chapman's admirable account of the feeding of young Brown Pelicans (2, p. 97) we learn that the naked young a day or two old takes its quota of pre-digested food from the front part of the pouch of the parent's bill, into which it has been regurgitated. Later, however, the nestling reaches far into the throat or gullet of the parent, thus exhibiting what may be called a feeding initiative.

In general this seems to be the usual method for all of the *Steganopodes*, unless there should be an exception in the Phaëthontidae. Chapman has observed the same method of feeding in the Booby (*Sulidae*), the Water Turkey (*Anhingidae*), and the Man-o-war-bird (*Fregatidae*). The Cormorants are also known to feed in the same way (2, p. 217). The same writer regrets not being acquainted with the feeding habits of the Tropic Birds (*Phaethontidae*) so that an inclusive statement might be made for the order. It is therefore unfortunate that Gross, in his most careful study of the Yellow-billed Tropic Bird (3), was not more explicit on this point. He dismisses the subject with the remark that "The food is transferred from the pouch-like gullet of the adult to that of the young by a process of regurgitation. This transfer of food is accompanied by a series of gulps, strains and wrigglings of the head and neck on the part of both birds." (3, p. 67). Attention will be called later to this description of the regurgitative process.

The Glossy Ibis, which belongs to the *Herodiones*, practices the same method. Baynard (4, p. 109) says: "The manner of the Glossy Ibis in feeding [its young] is to regurgitate the food up into the throat or mouth and for the young to put his bill, and many times his head, down the old one's throat and take his portion." As the young of this species grew older the parent would disgorge partially digested moccasins into the nest, and the young would pick up the food.

Very slightly differing from this is the account by Ward of the feeding of the young of the Herring Gull (5). Ward (quoted by Strong, 6, p. 37) describes the process as follows: "The young comes in front of an adult and with a bowing and courtesying movement puts up its bill to that of the old one, continuing the bowing for several minutes, resting between times. Sometimes it took hold of the adult's bill with its own, at other times merely touched bills. When the adult opened its mouth the young put its bill within. Failing to get indications of food, it went to another adult, and repeated the operation, passing in succession to several, until at length it seemed to get some favorable signs, for it remained by this one, alternately begging and resting. After some time it was apparent to me that the adult was striving to regurgitate. It would open its mouth, stretch nearly horizontally, then bring its head down to the ground. After a moment it would close its bill, turn its head to one side and look at the ground over which it had been straining, as though expecting to find something there. Other gulls were from time to time attracted to the scene, but were promptly chased away by this bird, who ran rapidly at them with open beak and outstretched wings. Perhaps half an hour after these efforts began I saw a portion of a fish appear in its mouth, and a moment later it was deposited on the ground, when the young promptly seized it . . . The adult assisted in breaking it up . . . The young fed mostly from the ground, but occasionally snatched a piece from the bill of the adult." Strong has made similar observations on this process in the same species (6 and 7).

In the second mode of nestling feeding which we arbitrarily recognize, the transfer of food is accomplished by the intercrossing of bills of the young and the adult, without the insertion of either. We find this method represented in at least three orders, viz., the *Tubinares*, the *Herodiones*, and the *Odontoglossae*.

In the case of the Laysan Albatross the bill of the young is placed crosswise between the mandibles of the adult. Partially digested food is then regurgitated and directed by the tongue of the adult into the open mouth of the young[2].

Among the *Herodiones* a somewhat similar method is found. Chapman (2, p. 121) has described the feeding process in Ward's Heron, the Florida Great Blue Heron, in the following words: "As the parent stepped into the nest, its bill was seized by one of the young. The young bird did not thrust its bill down the parental throat, nor was the parent's bill introduced into that of the young. The hold of the young bird was such as one would take with a pair of shears, if one were to attempt to cut off the adult's bill at the base. In this manner the old bird's head was drawn into the nest where more or less digested fish was disgorged, of which all the young at once partook."

The same author says the process of feeding the young of the American Egret is identical with that just described. Essentially the same thing is described by Gabrielson for the Bittern and the Least Bittern (8). But in these instances the food was not dropped upon the nest; it was, instead, passed directly into the young bird's mouth—perhaps a more refined and advanced process. His account for the Bittern is as follows: "As soon as she reached the nest the young commenced jumping at her beak, continuing this until one succeeded in seizing it in his beak at right angles to the base. A series of indescribable contortions followed, the head of the female being drawn jerkily in all directions and the muscles of the neck working convulsively. Finally the head and neck were placed flat on the nest for several seconds and then slowly raised again. As it [the head] came up the food came slowly up the throat into the mouth. As the food passed along the beak, the open beak of the young bird followed its course along until it slid into its mouth and was quickly swallowed. The young then released its hold and the parent stood with the muscles of the neck twitching and jerking." (8, p. 64).

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[2] I am indebted to Professor Homer R. Dill, of the University of Iowa, for the information regarding the use of the tongue by the adult albatross in feeding the young.

While the process is quite similar in the Albatrosses and Herons, one point of difference will be noted, viz., that in the former the beak of the nestling is placed crosswise between the adult mandibles, while in the latter the parent's bill is placed between the mandibles of the young.

In the Flamingo, belonging to the *Odontoglossae*, the feeding process may be referred to the same general plan, but with slight modification. The bill of the Flamingo is of such size and peculiar shape that the usual methods are not at all permissible. Neither bill is inserted in the other; nor would it be possible for the young to grasp the bill of the adult. So we find, in the words of Chapman (2, p. 187) that "What in effect is regurgitated clam broth, is taken drop by drop from the tip of the parent's bill." The food is really dropped from one bill to the other in a very dexterous fashion.

From the recent description by Gabrielson of the feeding process in the Rose-breasted Grosbeak, it might seem that there is in the *Passeres* a feeding process apparently belonging in this category (9). It would hardly be likely that this case could be related to those here described, but it is probably an adaptation of independent origin.

The third method of feeding which we will take into account consists of thrusting the food into the mouth or throat of the nestling by the parent bird. It appears to be the common method in the higher orders of birds, viz., the *Coccyges*, the *Pici*, the *Macrochires*, and the *Passeres*.

Perhaps the best analysis of this process has been given by Herrick (10) concerning the Black-billed Cuckoo. Food, which usually consists of insects, is placed by the parent well into the mouth or throat of the nestling. This act is a stimulus to the nervous mechanism of the young, and the response is a purely reflex act which sets in motion the pharyngeal muscles, thus accomplishing the deglutition of the food. The reflex act of swallowing is an automatic consequence of the contact stimulus on the throat or mouth. "This complex performance" says Herrick, "which represents the simplest sign language of the hungry bird, appears as a uniform chain-reflex, and is as predictable, and seems as mechanical as the response of the electric bell."

He points out, however, that this reflex does not long remain unmodified; that it may be inhibited by satiety, or accelerated by hunger. The rapidity of the reflex is dependent chiefly upon the hunger state; though it appears, in some cases, at least, to be necessary that the food be placed in contact with a certain region of the buccal cavity in order to provoke a prompt response. In one brood of Cuckoos with which Herrick worked he found it habitual for the adult to place its bill just within the tip of the nestling's beak, or place the insect food across between the mandibles of the young; in such instances the response was slow, the parent and young often remaining thus interlocked and motionless for five minutes by the watch, and commonly for two minutes .On the other hand, in another nest of the same species it was customary for the parents to place the food deep in the throat of the young. And here, says Herrick, " Every trial was a reaction test, and upon failure to swallow promptly, the food was withdrawn and another nestling was tested, precisely as in vireos, thrushes, and other passerine birds."

The exact conditions under which the parent awaits the reflex, or repeats the stimulus upon the same nestling, or carries the test to another bird, is a problem which may well be further investigated.

One of the interesting questions in connection with the feeding of passerine nestlings is as to the practice of regurgitation by the parents. It is quite possible that all of the passerine families are not uniform in their method of feeding the young. It is also quite probable that much of the difference of opinion in the matter is due to lack of agreement in terminology. It is, of course, important to know whether the passerine birds are uniform in this particular form of behavior.

The first necessity is the determination of the meaning of the word " regurgitation." It would perhaps not aid in our present purpose to attempt to analyse the different senses in which the term has been used by various ornithological writers, but we may at once resort to that court of appeals, the dictionary. The Century Dictionary defines the word as meaning " To pour or cause to rush or surge back." The Standard Dictionary gives the meaning as " To throw or pour back, as from a deep or hollow space; cause to surge back, as some mammals regurgitate food already swallowed."

These definitions seem to be eminently satisfactory, and I venture to presume that they will find approval in the judgment of most ornithologists. The idea of regurgitation, then, implies the previous act of swallowing of food, with concomitant reflex muscular activity. It seems reasonable to suppose that any reversal in the direction of passage would just as certainly require muscular action. And there is plenty of evidence to show that in the lower orders where true regurgitation occurs, such muscular action is clearly present. Let me remind you of the description previously quoted from Gross of the strainings and wrigglings of the head and neck of the Yellow-billed Tropic Bird in feeding the young; and of the muscular contortions of the bittern as described by Gabrielson. The photographs accompanying Fisher's account of the Laysan Albatross (11) indicate a raising and lowering of the head during the process.

Let us then consider that regurgitation cannot be accomplished without muscular effort, involving the pharyngeal muscles.

It may be objected that the position of all passerine birds in feeding is such as to permit gravitational regurgitation; that when the stomach and crop are higher than the head, the food may run down into the buccal cavity. Bearing in mind the collapsible nature of the esophageal walls when at rest, gravitational regurgitation does not seem to be a tenable hypothesis, and is not entitled to serious consideration until substantiated with some concrete evidence.

For the Coccyges Herrick's account of the life history of the Black-billed Cuckoo (10) is very complete. He makes no explicit statement as to regurgitation but the inference is easily drawn that he did not observe it.

In the case of the *Pici* the evidence for regurgitation seems to be good. Mr. William Brewster (12, pp. 233–235) gives a very complete description of the process of feeding the nestling of the Flicker. The parent approached the nest with the mandibles shut, no food visible; when the parent's bill was thrust into the nestling's throat there was a pumping movement accompanied by corresponding twitching of the tail and hinder parts of the body, and a slighter movement of the wings. As many as four young were usually fed at each visit. Similar testimony is given by Mrs. Miller (15, p. 18), by Baskett (13, p. 110), and by Burns (14, p. 54).

Passing on to the *Macrochires* we find that a considerable number of observations have been recorded.

In 1890 Mr. Brewster (16) described very vividly the feeding of the young of Hummingbirds in the following words: "Alighting on the edge of the nest, her tail pressed firmly against its outer side in the manner of a woodpecker, her body erect, she would first look nervously around, then thrust at least three-fourths of the total length of her bill down between the upraised open mandibles of the young bird. Next she would shake her head violently as if disgorging something; then, with their bills glued tightly together, both birds would remain, for the space of several seconds, perfectly immovable save for a slight, rapid, pulsating or quivering motion of the mother's throat. The actual contact of the bills lasted once for four seconds, once for six seconds, and twice for eleven seconds, the time being taken by a stop watch." . . . "The close and prolonged contact of the bills, the shaking of the mother's head, the subsequent quivering of the mother's, and, above all, the fact that after sitting on the nest for nearly an hour, she fed the young a second time without once leaving the tree in the interim, convinced me that the method of feeding was by regurgitation."

This testimony is confirmed by Shoemaker (17), for the same species, who says: "Very soon the mother bird appeared, and after a wary approach, alighted upon the edge of the nest and thrust her bill far down the throat of the young bird. I could see her throat move as she regurgitated the food. She left her bill in the little one's throat for about six seconds."

Such direct testimony cannot well be questioned without a careful re-examination of the circumstances. It should be borne in mind, however, that the length of the bill in the *Trochilidae* is a factor which must be taken into account. Even if the food, which probably consists of insects, were held in the mouth, or buccal cavity, we might suppose that some muscular action would be necessary to force it out along the mandibular tube and into the throat of the young bird. In Mr. Brewster's account it does not add to the proof that the parent did not leave the tree between feedings; since it might easily be assumed that the tree abounded in food material, i. e., insects.

We may also take into account the recorded observations of the feeding of young of the Nighthawk (belonging to the *Caprimulgidae*) which is in the same order as the Hummingbird, viz., the *Macrochires*.

Herrick watched the Nighthawk feeding its young, and says (18, p. 134) of the mother approaching the young ones: "She is loaded with fire-flies, and as her great mouth opens you behold the wide jaws and throat brilliantly illuminated like a spacious apartment all aglow with electricity. With wings erect and full-spread the old bird approached to within fifteen inches of my hand, making an electric display at every utterance of her harsh *ke-ark*. Then standing over her young, with raised and quivering wings, she put her bill well down into his throat and pumped him full. His down-covered wings were spread and a-quiver. In this position they remained interlocked and silent for one or two minutes."

Here is a case where, notwithstanding the interlocking of the parent and young for a brief period, the feeding cannot be regarded as regurgitation because the fire-flies were plainly seen in the mouth and throat as the adult approached. The question naturally arises now, may not other cases where the interpretation of regurgitation is based upon interlocking and slight quivering, be very similar to that of the Nighthawk? I am not aware that Herrick interprets this feeding process in terms of regurgitation.

Incidentally, we may note here the clear evidence of the fact that two families, at least, of the *Macrochires* feed as do the passerine birds, viz., by the insertion of the adult bill into the mouth or throat of the young. It is well to note this because of the occasional assertion that certain of the *Macrochires*, e. g., the *Micropodidae*, feed the young by taking the nestling's bill into the parental mouth.

We may now attempt to consider some of the evidence with reference to regurgitation in the *Passeres*. Perhaps the most extensive paper upon the subject is one by Mrs. Wheelock, published in 1905 (19). While this paper gives the author's observations in greatest detail, her conclusions are best summarized in the preface of her book on "The Birds of California," in which it is stated . . . "that young of all Macrochires, woodpeckers, perching birds, cuckoos, kingfishers, most birds of prey, and many sea birds *are fed by regurgitation from the time of hatching through a period varying in extent from three* *days to four weeks, according to the species.* Furthermore, that birds eating animal flesh or *large* insects give fresh (unregurgitated) food to their young at a correspondingly earlier stage of development than do those varieties which subsist on smaller insects or seeds. Also that exclusive seed eaters are usually fed by regurgitation so long as they remain in the nest."

"Out of one hundred and eighty cases in every instance where the young were hatched in a naked or semi-naked condition they were fed in this manner for at least three days. In some instances the food was digested, wholly or in part; in others it was probably swallowed merely for convenience in carrying, and was regurgitated in an undigested condition." There seemed to be no definite relation between the duration of the period of regurgitative feeding and the length of time required for full development of the young.

Mrs. Wheelock bases her paper in *The Auk* upon records of one hundred and eighty-seven broods (not species), in all of which the observations began on the day of hatching. The following families are represented in her records: *Fringillidae, Turdidae, Mimidae, Icteridae, Sittidae, Hirundinidae, Vireonidae,* etc.

Her method consisted in watching the nest at distances varying from ten to forty feet, though in some cases the distance may have been shorter; and in sampling the contents of the crop, immediately after feeding, by the insertion of a feather, and withdrawing such matter as adhered to it.

An adequate review of this important paper would be out of place in the present connection. The writer believes that the conclusions stated in the paper must be substantiated by repeated observations, since certain subsequent study has not been wholly confirmative.

As was suggested in Mrs. Wheelock's paper more notes have been published with reference to regurgitation in seed-eating birds. Thus, Wood (21) recently makes the statement that regurgitation occurs in the Goldfinch, although the evidence is somewhat circumstantial. Bergtold (22), in a very comprehensive and exhaustive account of the life-history and behavior of the House Finch, states that in that species the young are fed by regurgitation until they leave the nest (22, p. 59). A detailed description of the act of regurgitation is omitted, so that we are unable to judge what the author's conception of the regurgitative process is.

Miss Stanwood (23) incidentally states that the Olive-backed Thrush feeds by regurgitation. McAtee (24) states that Grosbeaks have been observed to feed the young by regurgitation; the same author elsewhere (25, p. 421; and 26, p. 342) takes very positive ground in favor of regurgitation, especially in the *Fringillidae*, but without offering any evidence.

We may now consider the negative testimony. Jones (27, p. 42) states that regurgitative feeding is never practiced by the Common Tern (*Sterna hirundo*).

Judd, in a very excellent account of the food of nestling birds (28, p. 412), while not explicitly discussing regurgitation, says that the first meal of the nestlings of the crow blackbird often consists of plump spiders of soft texture. Likewise, on page 425, the same author says that the first meal of the Crow usually is a young grasshopper, a plump spider, or a soft cutworm.

Jones (29, p. 69) reports the observations made by his students at the nestside of the Field Sparrow, the Song Sparrow, and the House Wren. He says: "There was no evidence that any of these birds fed by regurgitation. In the case of the sparrows this was clearly proved, but what might have happened in the case of the wrens can only be surmised. At any rate, the food was uniformly brought dangling from the bill and was not swallowed before being delivered to the nestlings. This was the case with the first feedings of both the Song Sparrows and the House Wrens."

Bigglestone (30) made a careful study of the nest life of the Yellow Warbler. All of the young were under observation within a few hours after hatching; but the last egg was under observation during hatching, and from that time onward the young bird was under constant observation till it left the nest. No regurgitation was observed, although this was one of the chief objects of the entire study.

A similar study was made of the Catbird by Gabrielson (31), in which two of the nestlings were under observation from the moment of hatching onward. Here also nothing suggestive of regurgitative feeding occurred.

During the summer of 1914 two similar nest studies were completed. The first, which has not yet been published, was undertaken by Mr. Jay Kempkes, who worked with the Western Meadow Lark (*Sturnella neglecta*) at the Iowa Lakeside Laboratory, on Lake Okoboji. Here also the results were negative, for no regurgitation was observed, although the birds were constantly under observation while in the nest; and in this instance one of the eggs was watched through the hatching process.

The second of these studies deals with the Rose-breasted Grosbeak (*Zamelodia ludoviciana*), and was carried on by Mr. Gabrielson at Marshalltown, Iowa. This report was published in a recent number of the *Wilson Bulletin* (9). The question of regurgitation was made the chief object in this study, because of the statement in one of the bulletins of the Biological Survey of the Government (24, p. 75) that the Grosbeaks feed their young in this way. The result of this very critical field study of the Rose-breasted Grosbeak was negative so far as regurgitative feeding was concerned.

While, doubtless, this review falls short of covering all of the literature on the subject, it may be sufficient to indicate that comparatively few studies have been undertaken on the passerine birds having expressly in view the question of regurgitative feeding. The writer believes the evidence is against this method in the passerine group.. There seems to be a field here for much interesting and valuable work.

The question will arise, What are to be the criteria in such a problem? The scientific attitude of mind is, no doubt, the first essential qualification on the part of the observer. It is perhaps no more important in any kind of ornithological inquiry than in this close and precise field work. Certain conditions must be observed. Among other things observation at close range is essential; and close range in this connection should mean two to four feet, with the nest not above the level of the observer's eye. The study should begin, preferably, with the hatching of the egg. Definite observation must be made as to whether, or not, the food is carried visibly in the parent bird's beak. It is true that McAtee (26, p. 342) claims that the visibility of the food, held in the mandibles of the bird as it visits the young for feeding, is no disproof of regurgitation. But as we have reviewed the numerous instances where unquestioned regurgitation occurs, we have not found it customary for such species to carry food in the mandibles. And in such a proper restriction of the term "regurgitation" as I have made in this paper, and as I believe the majority of ornithologists have been accustomed to use the term, it seems to me very improbable that birds which practice regurgitation would alternate with solid food. Food apparent in the bill may not disprove that the mouth is full likewise, and that the surfeit may extend well into the gullet; but that the removal of this surfeit from the throat or gullet is to be interpreted as regurgitation is quite beyond the limits of good terminology. I believe, therefore, that food visible in the bill is very good evidence against regurgitation.

One other point to be taken into account is the presence or absence of action of the pharyngeal muscles. While this may often be a little obscure and uncertain, especially for inexperienced observers, it nevertheless may be regarded as important circumstantial evidence. If muscular activity is clearly present a presumption is established in favor of regurgitation; but if no muscular activity can be determined such a presumption cannot be claimed, to say the least.

In conclusion I may be permitted to suggest that we may, in the future, find that there is greater significance in the comparative study of the manner in which nestlings are fed than has hitherto been recognized. Among the lower orders of birds we find a method of feeding the young which we will have little difficulty in regarding as primitive. In the higher birds, such as the Passeres, we find developed a distinctly complex performance. Between the primitive and complex processes alluded to, we find feeding methods which may be regarded as transition stages. Without, at this time, attempting a too rigid arrangement of these feeding processes, as to their natural and phylogenetic sequence, we may at least be justified in the conclusion that the problem deserves much further study. Whether any importance might be attached to such a quasi-physiological process in the determination of affinities it would be premature to speculate. But that this may be no more than a random suggestion, only future investigation can determine.

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Sioux City, Iowa.

A STUDY OF THE REACTIONS OF CERTAIN BIRDS TO SOUND STIMULI

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I. INTRODUCTION

This problem was undertaken at the Biological Station of the University of Michigan, under the direction of Professor R. M. Strong, between the dates of July 10 and August 21, 1916.

The Biological Station is located on Douglas Lake, in the western part of Cheboygan County, Michigan. The region immediately about the camp is covered with a fairly dense stand of young aspens, birches, and pin cherries, with occasional oaks and maples. This is the type of vegetation which has succeeded the original forests of pines and hardwoods in this cut-over and burned-over country. A few pines remain, chiefly along the lake shore, but there are no hardwoods in the immediate vicinity of the Station. Another important type of vegetation is found in the dense cedar bogs, where " arbor vitae, balsam, tamarack, and spruce form a nearly impenetrable jungle."

The bird life naturally shows a marked ecological concentration of species in these widely different habitats. In order that observations on any species might be made as nearly continuous as was desired, it was thought best to work with nesting birds as far as possible; and accordingly on July 5 search was begun for suitable subjects. But although birds are really fairly plentiful in the aspens during the early summer, the abundance of nesting sites furnished by so extensive and so uniform a habitat as the aspen association made the discovery of nests very difficult. In fact, it was not until the morning of July 8 that a nest was found located so that work could successfully be carried on.

The nest referred to was that of a hermit thrush. It was placed on the ground in a small cluster of oak seedlings, about a hundred feet from the shore of Douglas Lake. Work was begun here on July 10, and was continued until the young birds left the nest. By far the greater part of the summer's work was done on these hermit thrushes, because the nest was easily accessible from the Station, and because the hermit thrush proved a good subject for experiments of this sort.

Another nest, that of a robin, was discovered some days later, within the limits of the camp. Although for more than two weeks efforts were made to test the auditory reactions of this bird, it was found to be too timid for practicable experiments.

In addition some work was done in connection with this problem on birds found in the field, particularly on some of the birds characteristic of the cedar bog, and with some shore birds. Experiments were also made upon some young cedar waxwings which had been taken from their nest and placed in a cage for special study; but by the time that my experiments were begun the waxwings had become so accustomed to the presence of various people and to noises of all sorts that no positive results could be obtained.

II. METHODS AND MATERIALS

The experiments with the nesting hermit thrush were for the most part made with the aid of a small white observation tent which was pitched so that the apertures for observation were within six feet of the nest; and a narrow path from these apertures to the nest was cleared of grasses, etc., so as to admit the making of photographs. The tent was first pitched on the morning of July 10, and it was taken down the same day; on July 12 it was replaced and was left standing until all the work possible on the hermit thrushes had been completed.

The observations on the birds of the cedar bog and on the other birds experimented with in the open field were made without the use of any special shelter. Great care was taken to avoid other than auditory stimulation.

The sounds used were made as varied in character as possible. Those tried on the hermit thrush included shouting, singing, whistling both with the lips and with a "double-tone" metal whistle, chirping with the lips, clapping the hands, rapping on wood and on metal, and rustling papers and birch-bark. To test the reactions to sounds of different pitch a mandolin was used. The same sounds were also used in the case of the other birds, but such as involved sudden movement, as clapping the hands or rapping on wood or on metal, were not tried to any considerable extent. There is a possibility that auditory stimuli may sometimes have been accompanied by visual stimuli in the case of the thrushes when the giving of the sound required motion on my part. My blind was pitched between the nest and the morning sun, and the tent-walls were very thin, so that movements within it were often perceived vaguely from the outside.

The reactions to all these stimuli were more or less similar, differing in degree only. In every case they consisted of movements of the head and of the bill, of raising the wings, and of winking. The eye-wink, however, is of doubtful value, and was considered only in the case of the thrushes. The interval between the giving of the stimulus and the perception of the reaction to it seemed fairly constant for those birds which reacted at all, being about three-fourths of a second, as nearly as could be determined.

III. OBSERVATIONS

1. On the nesting hermit thrush. July 10, 9:10–10:50 a. m., 1:30–3:20 p. m. The bird was not much alarmed, even at the very first, by my stirring about in the tent, but flew when, at 9:20, I caused the side of the tent toward the nest to flutter. It returned in two minutes, and took its usual position on the nest, facing the tent obliquely, with its head turned toward the woods, to which the bird always went on leaving the nest, rather than toward the lake. Only rarely, and then usually in response to sound stimuli, did it turn its head directly toward the tent. I never saw it approach the nest except from the side *toward* the blind.

The first time that I released the shutter of my camera the bird showed decided alarm, but this was of short duration, less than three seconds. Rapping with a pencil on the metal cover of my note-book caused the bird to turn its head from side to side, as if it were trying to locate the source of the sound. A short blast on the whistle caused the same reaction, apparently of about the same intensity; when this experiment was repeated the same result was obtained, but after the tenth trial the bird seemed to have become accustomed to it, and the only response it made was merely to assume a more alert attitude.[1]

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[1] Similar observations were made by Strong on gulls studied from a blind. Strong, R. M., 1914. On the Habits and Behavior of the Herring Gull, *Larus argentatus* Pont. *The Auk*, vol. 31, Nos. 1–2, pp. 22–49, 178–199; plates 1–10, 19, 20, also *Smithsonian Report*, 1915, pp. 479-509.

Even so faint a sound as that made by my pencil in writing on the note-book page seemed to cause the bird some uneasiness. Singing caused very slight apprehension, not nearly so much as did the sound of the waves thrown up on the shore by a passing launch. At the second release of the camera shutter the bird showed less concern than was evident the first time; but when I moved the camera in winding the film, it was alarmed to the point of standing in the nest, and it even walked off while I was rewinding the shutter curtain. It was gone only five seconds.

In the afternoon a companion accompanied me when I returned to the blind. The bird stayed on the nest when we entered the tent; but when I moved my finger in the aperture it showed great alarm, and left the nest when I flashed a mirror there: it was gone seventeen minutes. On its return I waited for several minutes before attempting any experiments. I noted that the bird was always on the alert, particularly for sounds from the tent; however, it was not insensible to other sounds, for several times it took food, usually large ants, from the edge of the nest, apparently in response both to auditory and to visual stimuli; the thrush seemed to be made aware of the ant through an auditory stimulus, and then to discover it through the visual sense. The bird seemed also to start visibly at sudden noises from outside the tent; but on this date it was concerned chiefly with those which were made within the blind.

The day was clear and warm, and the bird panted considerably. I found that usually it would close its bill when I made a sudden sound, and would turn its head and wink its eye, while to sounds from outside the tent the response consisted usually in merely turning the head. The bird sometimes turned its head at our conversation, but usually it paid no attention to it; once it seemed quite disturbed at the noise made by tearing birch-bark. My companion left after half an hour in the tent.

The slightest movement of the tent-wall near any of the apertures was sufficient to attract the bird's attention, but it seemed only slightly concerned by the movements of the canvas elsewhere. A sudden gust of wind sounding in the pines overhead caused the bird to start slightly, and soon afterward it started noticeably at a junco's song from the same trees. Then, later, when I tapped on my note-book cover with my pencil, the bird looked about over its head as if trying to discover the source of the sound.

During the afternoon I tried the effect of song on the bird, but I obtained no positive results. I did notice, though, that if the song were suddenly broken off and two or three sharp raps given on the tent pole, the bird reacted more vigorously than to the raps alone. And a suddenly *ended* loud sound seemed to startle it more than a sudden loud sound did ordinarily. These reactions were noticed several times during the afternoon, but they became much less marked on successive repetitions of the experiment.

July 12, 9:25–10:40 a. m., 1:10–3 p. m. The bird seemed very uneasy at noises made outside the tent, particularly at the loud cawing of some crows. After about half an hour of quiet, I blew a loud blast on the whistle, which produced only a slight reaction. The squeaking sound made by kissing the back of the hand vigorously produced no visible reaction. The higher pitched of the two whistle notes, when sounded alone, seemed to produce a slightly more vigorous reaction than did the lower one alone. But no whistle blast produced so strong a reaction as did the sudden loud call of a cuckoo from the near-by aspens.

The visual stimulus produced by a moving object seemed very much stronger than did any auditory stimulus; when I showed my fingers at the aperture the bird showed very decided alarm. As the experiment was repeated the reactions became much less pronounced.

In the afternoon I took a mandolin to the tent; and, as with the whistle, the notes of higher pitch seemed to produce slightly more vigorous reactions. However, the differences in the reactions were so slight that it was very difficult to make such determinations. The notes used ranged over about two octaves, from the open G-string of the mandolin to B two octaves higher.

I found that a chord produced a more vigorous reaction than did any single note; however, the bird quickly became accustomed to the chord, and after half a dozen trials merely showed increased vigilance. As on July 10, I found that if a sound was interrupted by another of very different character, a more vigorous reaction was produced than by mere suddenness or loudness of sound. After the bird had become accustomed to the mandolin and to the whistle so as to react to them only slightly, I tried the effect of interrupting the mandolin chords by loud whistle blasts, and found that the bird reacted markedly, though with decreasing vigor as the experiment was repeated.

I experimented also on the combination of auditory with moving visual stimuli. As stated above, the sudden appearance of my finger at the aperture seemed to startle the bird, but the reaction decreased rapidly in vigor on successive trials. The same was true of the reaction produced by sounding the open G-string of the mandolin. If, however, I showed my finger at the aperture, then, after a short pause, moved it suddenly and at the same instant sounded the G-string loudly, the bird reacted vigorously; and *the reaction was as strong at the thirtieth trial as at the first.*

July 13, 8:45–10:20 a. m., 1:10–3:20 p. m. The work in the morning was similar to that of the two days previous, and the reactions observed were similar, though less vigorous on the whole. The combination of auditory and visual stimuli was tried again, and the same results were obtained by combining the movement of my finger with a loud whistle blast as with a mandolin sound; although fifteen trials were made, there was little, if any, diminution in the vigor of the reaction, which in this case consisted usually in turning the head and closing the bill momentarily.

In the afternoon I approached the nest from the side opposite the tent. I crept up over a thick growth of bear-berries without taking particular pains to move quietly, so that I am sure that the bird must have heard me. The bear-berries screened me from the nest, so that until I came within three feet of it I could not see the brooding bird. I found that the bird seemed not at all on the alert for any disturbing sound from the tent, nor had it seemed to notice my approach. I then blew a loud blast on the whistle, but it showed no sign of fright, and merely turned its head slowly until it caught sight of me, when it immediately left the nest.

I then concealed my watch carefully about six inches from the nest, and immediately entered my tent. When, after fifteen minutes, the bird returned, it was very plainly made uneasy by the ticking of the watch; it turned its head from side to side, and looked for it when once its approximate location had been determined from the sound. After about half a minute, however, the bird gave up the search and paid no more attention to the watch.

The bird now seemed constantly on the alert for sounds from the tent, having seen me enter it; very slight reactions were noticed, however, to whistling, shouting, and clapping the hands, while rapping on wood and chirping with the lips produced no visible reactions.

July 16. The three eggs hatched this afternoon. I made no observations.

July 17, 8:40–9:30 a. m., 1:10–3:10 p. m. There was no sign of either parent during the fifty minutes I spent in the tent in the morning. In the afternoon one of the parents was at the nest when I approached, and stayed while I entered the tent. On this date, for the first time, I obtained a response to the chirping sound. To it the bird responded by turning the head, often as much as 90 degrees, and by winking. Although the interval between winks varied between such wide limits as two seconds and thirteen seconds, I think that the wink can safely be considered as a part of the reaction, since in each case it accompanied the turning of the head, about three-fourths of a second after the sound stimulus was given.

To the higher-pitched of the two whistle notes the bird again reacted slightly more vigorously than to the lower; the reaction here consisted in turning the head and closing the bill. The reaction to this sound was on this date much less vigorous than that to the chirping.

I tried a new vocal sound successfully; a rapid, rolling "rr-r-r-rr." To this the bird responded on six out of seven trials, showing alarm not merely at the beginning of the sound, but as long as it was continued.

The experiment of changing from one sound to another of a different sort gave results this day on only three trials out of seven. However, the bird seemed more responsive to all other tests than on the last day that observations were made before the hatching of the eggs.

July 19, 9–10:40 a. m. The young birds' eyes were just opening when I began my observations. Any small sound from the tent seemed to stimulate the nestlings to raise their heads as if for food; and I noticed that in this connection such sounds as rustling paper or birch-bark were stronger stimuli than were sharper sounds such as tapping or chirping. When the parent returned it stood in the nest over the young, and was continually on the alert. The usual sound stimuli were tried—tapping, whistling, clapping the hands, etc.—and the usual reactions were secured. Interrupting a sound by another of a different sort produced vigorous reactions twice in three trials. For the first time since July 10 the bird seemed to be made uneasy by the sound of my pencil; when I started writing it gave a slight reaction, and again when I stopped writing. This was the first day since July 10, however, when the wind was blowing from the tent toward the nest.

When I made my first photographic exposure this morning, the parent on the nest had ceased momentarily to watch the tent and was bending over the young. The sound of the camera aroused it to watchfulness again. Subsequent releases of the camera shutter did not seem to attract the bird's attention at all.

July 20, 9:10–10:50 a. m. While the parent was absent I tried the effect of a loud whistle blast on the nestlings. At the first trial one of them raised its head, but five subsequent trials produced no effect.

When a parent returned I made some experiments to determine to what extent reactions were inhibited when the bird was at the nest. While it was approaching the nest and when within a few inches of it, I tried various sounds, but without effect. When this bird had finished feeding the nestlings, I gave a loud whistle blast, and the bird started visibly. Later, when a parent approached the nest again, and was still five or six feet away, I tapped my note-book cover with my pencil, with the result that the bird turned and ran off some fifty feet. When it returned a minute later I repeated this experiment, and the bird flew away and was gone several minutes. After several feedings I made some further experiments, with the following results: when the parent was coming to the nest and was within a few inches of it, or when at the nest-side and engaged in feeding the nestlings, it seemed to pay little or no attention to sounds from the tent; but after the young were fed and the nest was cleaned, it seemed always to notice them. Yet it was by no means as responsive (on this date) to any sounds from the tent as to the very faint lisping sounds with which the young asked for food.

July 21, 8:30–10:45 a. m., 1:20–2:30 p. m. One of the nestlings was lying in the nest, when I entered the tent, with its head raised and bill opened so that the lower mandible lay on the edge of the nest. I clapped my hands several times at considerable intervals, and each time the young bird responded by raising its head nearly to a vertical position and closing the bill slightly. When a parent returned I repeated the experiments of the day before, and again I found that the reactions were greatly inhibited when the bird was at or near the nest, and that the bird when at the nest seemed to pay much more attention to the sounds made by the young than to any sounds I made. In the afternoon I repeated experiments on the nestlings, but the only response obtained was similar to the one just described.

July 24, 8:05–11 a. m. During the first fifteen minutes of the period the young were very quiet. I observed that whenever I made any sudden loud noise, one of the nestlings invariably raised its head, opened its eyes, and (apparently) watched the tent for a few seconds. If the sound were repeated, it did not show any further alarm, but merely continued to watch the tent for a somewhat longer period than if the sound were not repeated. I also noticed that the nestlings never seemed to be aware of the approach of the parent, whether it ran or flew to the nest-side; and it was my experience that its flight was very noisy, with loud whirring of the wings, when it approached the nest. In direct contrast to this was the case of some cedar waxwings which came to my attention during the summer; here the nestlings seemed always to be aware of the parent's approach at a distance, and for some time were in a state of expectancy.

Except in the cases mentioned in the preceding paragraphs I was never able to obtain any marked response from the nestlings to sudden and loud sounds. This seems to me to be directly contradictory to a statement of Lloyd Morgan (Animal Behavior, p. 49) to the effect that young birds " show signs of alarm at any sudden and unaccustomed sound." After I had been in the tent twenty minutes and the young birds had become entirely quiet, I repeated the experiments with various kinds of sounds, as whistling, rapping on wood and on metal, clapping my hands, etc., but I was unable to detect any positive reactions.

I also continued the observations on the inhibition of reactions in the parent when near the nest, with the same results as before.

July 25, 8:25–10:30 a. m. The observations made from the tent this morning were substantially the same as those of the day before, except that for the first time I was sure that both parents came under my observation. I was not able to detect any difference in their behavior.

At 9:45 I left the blind and withdrew for about ten minutes. On my return I waited until a parent had finished feeding the nestlings and had left the nest, and then, instead of going to the blind at once, I took advantage of some natural cover to conceal myself. Neither of the parent thrushes seemed to pay the slightest attention to me on their subsequent visits to the nest, nor did either of them respond visibly to any sound that I made, though I tried shouting, whistling, and chirping loudly. But after I reentered the tent (at 10:15) I found that both birds reacted markedly to these same sound stimuli.

2. Observations on a young hermit thrush. In the late afternoon of July 26 a young thrush was taken from this nest for the purpose of studying its reactions to sounds under laboratory conditions. On this date it gave no evidence of reactions to sounds or of the formation of associations between sounds and other events. On the two days following there was no opportunity to study this bird.

On July 28, a very warm and sultry day, the bird became sick, due doubtless to the heat and to the change in environment and feeding; it was transferred to a more airy cage. The next day the temperature was still higher and the bird was still sick; yet it was very active, and made violent efforts to escape from the cage, with the result that it so nearly exhausted itself that it was practically unable to open its eyes. It was on this date that the first observations were made which showed any ability on the part of the bird to associate sounds with other events. For instance, after the bird had been fed four times, it was noticed that when the door of the cage was rattled the bird turned toward it at once and begged for food. If food were not forthcoming, this reaction became less and less vigorous on successive trials, and finally ceased altogether until the bird had been fed again. In the afternoon of the same day the thrush was taken outside the cage; and even under these conditions, and when at some distance from it, the bird continued to orient itself toward the source of the sound and to beg for food when the cage door was rattled. During all of these experiments the bird kept its eyes tightly closed.

Further experiments were planned, but the thrush died on July 30.

3. Observations on birds of the cedar bog. On August 13 I went down into a dense cedar bog about two miles from the station, and, while in the more open parts, I ran across a flock of chickadees, golden-crowned kinglets, and brown creepers, numbering perhaps thirty individuals. I tried the effect of whistle blasts, of clucking with the mouth, and of shouting, all at a distance of less than fifteen feet, without obtaining a positive reaction from any of these birds; nor did this surprise me, when the fearless habits of these birds were considered. When I clapped my hands, however, a kinglet did fly to a farther tree; but this was undoubtedly due rather to the effect of the visual than to the auditory stimulus. Later I tried the effect of a whistle blast on a black-throated green warbler, with more positive results. The bird raised its wings as if to fly, but soon settled back and then continued its search for food. Subsequent trials produced no result.

4. Observations on young cedar waxwings. As was stated in the introduction, these waxwings were so accustomed to sounds of all sorts before my experiments were begun that almost no positive results were obtained. In fact the only thing definitely established was that these birds were more responsive to sound stimuli before being fed than afterward.

5. Observations on certain shorebirds. On August 21, I made a series of observations on some solitary sandpipers, least sandpipers, and kildeers which were feeding on the beach near camp. I tried whistle blasts, shouts, and percussive sounds, both vocal and clapping my hands. The only reaction I observed among the sandpipers was given by a solitary sandpiper, which

raised its wings when I clapped my hands. To the whistle blasts the kildeers responded at first by running a few steps along the shore, but later they gave no reaction to this sound. To cluckings they did not respond, but when I clapped my hands the whole flock took flight. The visual stimulus undoubtedly was the stronger in bringing about this reaction.

Later I made similar experiments on a solitary kildeer, without obtaining any positive results.

IV. SUMMARY

1. The hermit thrush was constantly on the alert as long as I was in the observation tent, and while I was there it seemed very often to be more sensitive to sounds from without the tent than to those which I made inside.
2. If a continued sound were suddenly interrupted by another loud sound of a very different character, the bird reacted more vigorously in most cases than to either sound alone.
3. The hermit thrush seemed not particularly sensitive to sounds when no one was in the tent.
4. An auditory stimulus produces a much stronger reaction in birds when it is reinforced by a moving visual one, and a moving visual stimulus when it is reinforced by an auditory stimulus.
5. The hermit thrushes under observation very soon became accustomed to various sounds and in a short time ceased to react visibly to them unless the sounds were reinforced by other stimuli.
6. The hermit thrush was very much more sensitive to sound stimuli early in the period of experimentation than later, and there was a secondary maximum just after the hatching of the eggs.
7. The reactions to sounds on the part of the hermit thrush are very much inhibited when the bird is at the nest or within three feet of it, but this inhibition is much less after the young are fed than before.
8. The adult hermit thrush is apparently more sensitive to notes of higher pitch than to sounds of lower pitch.
9. Very young birds were more influenced by such sounds as the rustling of paper or of birch-bark than by sharper sounds such as tappings, whistling, etc.

10. I found the young of the hermit thrush during the first ten days after hatching very little influenced by sound stimuli.

11. A thirteen-day old hermit thrush very quickly learned to associate certain sounds with feeding.

12. Shore birds, chickadees, golden-crowned kinglets, and brown creepers observed in the field were not visibly influenced by sound stimuli. A slight response was obtained from a black-throated green warbler.

13. From a rather unsatisfactory study of young cedar waxwings it appears that they are more sensitive to sounds before being fed than afterward.

CHOICE OF FOOD IN AMEBA

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INTRODUCTION

In a previous paper ('16a) I outlined the problem of choice of food among animals as I conceive it, and in this paper I wish to discuss the power of choice in ameba as exhibited in the various series of experiments recorded in several of my previous papers, as well as in experiments which are recorded for the first time in this paper.

The problem of choice of food has turned out to be very intricate and difficult; much more so than was at first suspected. It is rendered especially difficult because previous experience in sense perception plays a very important part in selection. Choice thus becomes in large part a developing or historical process. Series of individual acts of choice are the smallest units which can be considered in analyzing this problem. Individual acts of choice are frequently quite meaningless, and even contradictory to each other, when removed from their historical setting. This fact is of the greatest importance in this connection and must not be lost sight of.

Before a discussion of choice of food is entered upon, I wish first to describe two series of experiments which have particular bearing on this matter. One series has to do with choice expressed by an ameba when encountering two particles of different composition lying very close together, while the other series deals with the effect of mechanically agitating various kinds of particles in close proximity to the ameba.

REACTIONS TO TWO PARTICLES OF DIFFERENT CONSTITUTION LYING CLOSE TOGETHER

Globulin and silicic acid.[1]—A grain of globulin and a grain of silicic acid were laid close together in the path of an Amoeba proteus[2]—figure 1. The test objects were laid some distance ahead so that all the changes in behavior due to the test substances could be observed. The ameba moved directly forward for a considerable distance, then sent out on either side several pseudopods which were, however, soon retracted—3. As the ameba moved further forward toward the test substances, it broke up into three pseudopods, the middle one of which pointed directly toward the silicic acid, though it did not move into contact with the acid—5. The right-hand pseudopod was retracted while the ameba moved on through the pseudopod on the left, gradually swinging around the silicic acid, and coming into contact with the globulin from the opposite direction. The globulin was ingested without the formation of a food cup, while the silicic acid was carried to the back of the ameba where it remained a short time.

Silicic acid and egg albumin.—The ameba whose reactions to globulin and silicic acid were described above, later reacted positively to, but finally avoided, a capillary tube containing a solution of egg albumin—14. After this test a grain of silicic acid was laid in front of the tube of albumin—26. The ameba moved toward the silicic acid until within about fifty microns of it when there were formed several side pseudopods, of which the one on the right became the main pseudopod. But this one soon curved to the left and toward the silicic acid, and then kept on moving in this direction until within thirty microns of the acid when the tip of the main pseudopod turned slightly to the right and moved past the test object—35. But as soon as the tip of the ameba was well past the silicic acid, the ameba turned toward the open end of the tube and a small pseudopod was also sent out toward the tube—38. The ameba, however, moved away from the tube of albumin through a pseudopod sent out on the right. This experiment demonstrates very clearly that, although the mere presence of a solid object immersed in a solution of some other substance serves to attract an ameba, the main factor in determining the movements of an ameba is either the increasing density of the diffusing molecules or ions as the source of diffusion is approached, or some other physical disturbance propagated radially from the source of diffusion.

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[1] For method of preparation of the test substances mentioned in this paper reference should be made to my former papers, '16b, '16c.

[2] For a description of the species of ameba mentioned in this paper refer to my paper '16d, in Science. In previous papers I spoke of 'raptorial' and 'granular' amebas. Raptorial amebas are of the species Amoeba dubia Schaeffer, while the granular amebas refer to two species: Amoeba proteus Pallas emend. Leidy, and Amoeba discoides Schaeffer. From my notes I am unable to tell in all cases to which of the latter two species the granular amebas belonged. This is due to the fact that discoides was not discovered to be distinct from proteus until after these experiments were made. In this paper therefore, the label A. proteus includes also the species discoides.

(Figures 41-50 represent a control experiment showing that silicic acid by itself does not cause a positive reaction.)

Globulin and soluble egg albumin.—In an experiment similar to the preceding, on the same ameba, but in which a grain of globulin was used instead of silicic acid—51, the ameba moved away from the tube of egg albumin after the globulin was eaten—65. This experiment, when studied in connection with the preceding experiments upon this ameba, shows very strikingly the nice discriminations in the selection of food which this animal is capable of making.

Carbon and lecithin.—The lecithin bore Merck's label and was made from eggs. A small amount of it was smeared on a carbon grain which was then laid in the path of an A. proteus—101. The ameba moved forward into contact with it, and then moved off through a pseudopod which had been forming on the left—107. The carbon-lecithin was then shifted—109. The ameba moved toward the test object, then turned toward the left, then moved forward into contact with it again, and then moved on leaving the carbon-lecithin behind. A new piece of carbon, with fresh lecithin was then placed near the ameba—115. The ameba moved forward into contact with it and then passed on. A small pseudopod was thrown out posterior to the carbon-lecithin, and later another anterior to it, but the ameba finally moved away without attempting ingestion.

Globulin and lecithin.—A grain of globulin was smeared with lecithin and placed in the same ameba's path—123. The ameba moved forward a short distance toward the test objects, then turned to the left, avoiding them.

Globulin and hematin.—A grain of hematin and a grain of globulin were laid close together in the path of an A. proteus—67. As the ameba moved forward a pseudopod was thrown out on the left toward the globulin-hematin. A food cup was formed and both substances were ingested. There was no period of rest, the ameba moving on in the same direction. The hematin remained in the ameba's body for a considerable time thereafter. A little later another grain of hematin and one of globulin were laid in the ameba's path—78. The ameba moved into contact with them and carried them up on its back—82, and then formed a food cup extending upwards and ingested them. The ameba remained comparatively quiet for a short period, then moved on in the original direction. Another grain of hematin was then laid with a grain of globulin some distance ahead of the ameba—87. The ameba moved forward toward the test objects and when within about seven microns of them—91, 92—the tip of the main pseudopod spread out and formed a food cup over them just as if they were moving organisms like flagellates. The food cup was completed and the hematin-globulin taken into the protoplasm as on the two previous occasions. The ameba quieted down for a few minutes, then moved off about thirty degrees to the left of the original direction.

No attempt was made by the ameba in any of these experiments to separate the globulin from the hematin and to ingest the globulin only, leaving the hematin behind. But it is to be noted that in all these experiments the globulin grain was much larger than the hematin. The most remarkable incident is the ingestion in a food cup—93, 94—where the food cup was formed before the ameba had come into actual physical contact with the hematin or the globulin.

Globulin and uric acid.—A large grain of globulin and a small grain of uric acid were laid close together in the path of the ameba used in the experiment with hematin and globulin recorded above—129. The ameba moved forward into contact with the globulin-uric acid and ingested them without the formation of a food cup. The ameba remained quiet for about five minutes, after which it moved off in the original direction.

Globulin and carbon.—A small grain of carbon was laid on a larger grain of globulin in the path of an active A. proteus—138. The ameba moved forward in Y-form with the carbon-globulin lying between the prongs. The right prong finally became the more active and in its forward movement dragged the retreating left prong into contact with the globulin-carbon—147. A pseudopod was then sent out against the test substances which upset them so that the carbon lay between the ameba and the globulin. A large food cup was then formed over both substances—149. The carbon grain was soon pushed out of the food cup while the globulin was taken into the protoplasm. Just how this happened could not be determined, but it was not "accidental."

Another grain of carbon together with one of globulin of about the same size, were laid in the path of an A. proteus—151. The ameba moved forward to the right of the test substances—153. A side pseudopod was then sent out to the left. It passed the carbon on the left. A small pseudopod was then sent out into contact with the globulin grain—157. A large food cup was then quickly formed over the globulin-carbon—158—but presently the carbon was pushed out while the globulin was taken into the protoplasm. The details of the separating process again could not be observed.

A grain of globulin was then placed on a large grain of carbon in the path of a large ameba belonging to the proteus species—159. As the ameba moved forward a pseudopod was thrown out on the left—160, but it was soon withdrawn—162. The main pseudopod flowed on past the carbon-globulin and then turned sharply to the right—164. A small Y-shaped pseudopod was sent out toward the test substances as the ameba moved away, but it was retracted before it had covered more than half the intervening distance—164. The grains of carbon and globulin were then shifted—165. The ameba moved past them a short distance—168. The tip of the main pseudopod then turned to the left and moved into contact with the test substances. The carbon-globulin grains which were sticking together slightly, were rolled around a few times by the ameba. A food cup was then formed with the test substances lying, not in the food cup, but in the mouth of it—172. Half a minute later another food cup was formed over them, but the ameba did not fuse the free ends of the cup until four minutes after forming it—172. The ameba then quieted down for about thirty-minutes, during which time but very little movement could be observed; nevertheless the globulin and the carbon became separated from each other, the carbon lying in the anterior half and the globulin in the posterior half—178. The ameba then moved off in the direction opposite to the original, but so that the carbon should at once occupy a position at the posterior end. A few minutes later the carbon was excreted. Ten minutes after the ameba had enclosed the carbon and the globulin in the food cup, another normal food cup was formed while the ameba was lying quiet, but there was no solid substance in it, nor was there anything in the vicinity to cause its formation. The stimulus producing it must have been internal.

This is a remarkable series of experiments. A degree of precision in food discrimination is disclosed in these observations which was altogether unsuspected. The separating process in the first two experiments is not understood. Not all the details necessary to an understanding of the process were observed. The ameba reacted like a higher animal might if reduced to ameboid form. The last experiment clearly indicates that the ameba was "aware" of the presence of a particle that was not food lying close to one that was food. The way in which the first food cup was formed clearly shows this. The long delayed fusion of the free edges of the food cup indicates the effect of the disturbing carbon. The long rest of thirty minutes also is unusual. The change in the direction of locomotion was doubtless caused by the position of the carbon. And the formation of the empty food cup during the resting period was in some way incited by the disturbing carbon, but just what connection there might be between the two remains unknown.

Gluten and glass.—In the path of an A. dubia that had just previously ingested pieces of agitated glass, was placed a piece of glass and a piece of gluten lying close together—179. The ameba moved into contact with the gluten and the glass—184-186—and then carried them up on its back, but there was no attempt to ingest either of the substances.

Globulin and Coleps hirtus.—A small mass of metallic iron was temporarily attached to a grain of globulin and slightly agitated with an electric coil. The Amoeba dubia near which the globulin lay, nevertheless treated it with indifference. A coleps then came along, and while hovering over the globulin, both the globulin and the coleps were ingested by the ameba in a food cup thrown out from the posterior end—190. Five minutes after the formation of the food cup the coleps stopped moving, and at the same time the water disappeared from the food vacuole. The coleps became separated from the globulin, and about twelve minutes after the food cup was formed the globulin was excreted.

The results of these experiments leave no doubt of the fine sense of discrimination which ameba is capable of exercising. Not only does ameba discriminate before coming into contact with objects, but also after they are in the food cup and even after they are imbedded in the protoplasm. The experiment recording the ingestion in the same food cup of globulin and a coleps indicates this, for after these substances were imbedded in the protoplasm a coleps was preferred to globulin.

The experiments with egg albumin and globulin, and egg albumin and silicic acid, show clearly that the presence of a substance in solution only is not sufficient to attract ameba, nor to cause ingestion, but that the substance must be actively diffusing from a definitely localized region.[3]

THE EFFECT OF MECHANICAL STIMULATION

It became evident as the feeding experiments went on that movement of food objects is an important factor in ingestion, and sometimes indeed a determinining factor. A number of experiments were then projected to see especially what the effect of water vibrations is upon ameba, and whether vibrations of themselves are capable of causing a definite change in behavior.

It is to be regretted that but few drawings can be presented in illustration of the gradual change in behavior that is produced by mechanical stimulation; but it was impossible to make a series of drawings for each experiment, as was done in the other cases, for the drawing hand of the experimenter was employed in vibrating the needle. Consequently with the exception of one experiment—194-197—which is represented by memory drawings made immediately after the experiment, only the final stages are illustrated by camera lucida figures. The different kinds of objects used in these experiments are fairly representative. Several kinds of insoluble indigestible substances, as well as food substances, were employed.

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[3] There is some evidence here that two particles of different degrees of attractiveness when encountered separately, are reacted to, when lying close together, as one (the more attractive) being attractive and the other (the less attractive) repulsive.

The effect of vibrating food particles.—A small fragment of an ameba was placed in the path of an A. proteus. Pseudopods were sent out toward the fragment, but all of them were soon withdrawn—198-205. The fragment was then allowed to roll down the side of the ameba, whereupon ingestion followed at once—206. It is certain that the mechanical stimulation produced by the rolling fragment hastened ingestion.

An A. dubia was then tested ten times with grains of globulin, but only one was eaten, the seventh. On the eleventh trial a piece of globulin was laid against a newly formed pseudopod and agitated with the point of a glass needle. A food cup was promptly formed and the globulin apparently ingested—207. Five minutes later the ameba moved on, leaving the globulin behind in about the same place—210. It had not been completely surrounded by protoplasm. The formation of the food cup in this case was caused by the vibration of the globulin.

Another A. dubia that reacted rather indifferently toward globulin, although the globulin was finally eaten, and quite indifferently toward ovalbumin, iron and fibrin, was tested with a grain of fibrin agitated with a glass needle. A food cup was formed and the fibrin apparently ingested at once in a food cup containing a large quantity of water—211. The ameba became quiet for a minute and a half and then moved off in the original direction, leaving the fibrin behind, four minutes after the formation of the food cup—212-216. The fibrin was probably not completely surrounded by protoplasm. The formation of the food cup was caused by the vibrations of the fibrin.

The effect of vibrating alga filaments.—One of the most illuminating experiments bearing on the general problems of mechanical stimulation is the following: A raptorial ameba which had reacted indifferently to capillary tubes filled with peptone solution was gently stimulated mechanically by the free ends of three thin oscillatoria threads wrapped around a glass needle. Stimulation at the posterior end produced a prompt reversal of streaming. When stimulated at the newly formed posterior end, streaming was again reversed. In this way the direction of the protoplasmic current was reversed eight times in succession, the current always moving toward the point of stimulation, without bringing the ameba away from its original location. Figure 217 shows the position of the ameba while the protoplasmic current was changed four times. The sides of the ameba were then stimulated at various places with the alga threads and at each point a pseudopod was thrown out. If the stimulating was done properly, food cups were begun at these pseudopods. Partial or complete food cups could be formed at will, depending upon the character and continuance of the stimulus. In short, all the ordinary items of positive reacting, from simple movement toward a stimulus to the prompt and complete formation of a typical food cup, could be produced by varying the intensity, frequency, and character of the stimulus. The mechanical stimuli proceeding from the alga threads were probably the only ones concerned in producing the reactions described, for the bottom of the dish was strewn with broken oscillatoria filaments, over which the ameba frequently flowed without changing its behavior. It was only when the filaments were agitated in contact with the ameba, or nearly in contact with it, that the ameba responded with a positive reaction. The efficiency of this sort of stimulation lies doubtless in the fact that the great flexibility of the alga threads permits one to simulate to a high degree the movements of small living organisms.

An experiment similar to this one gave almost identical results. A large binucleate A. proteus that had reacted indifferently to globulin grains or eaten them imperfectly was stimulated with the alga threads and the response was the formation of a complete food cup—FC_1, 220. The ameba was stimulated again and another food cup was started, FC_2. A grain of globulin was then dropped into the partly formed food cup and upon further stimulation the food cup closed completely. The globulin was retained for over two hours, when observation was terminated. The first food cup which was formed, it is interesting to note, remained almost undiminished in size for over two hours. It remained much longer than if it had contained food.

In another experiment of a similar nature the glass needle was used without any alga threads or anything else on it—194. The point of the needle was agitated near, *but not in contact with*, an A. proteus. A pseudopod was promptly started in the stimulated region—195, and it attained to considerable size and finally formed itself into a food cup, which was, however, not completed—197. The needle at no time touched the ameba. This experiment, in connection with the preceding ones, shows that *a purely mechanical stimulus is sufficient to set in operation the ameba's feeding mechanism.*

The effect of vibrating insoluble indigestible particles: Glass.—A clean piece of glass was laid near an A. dubia and slightly agitated with a clean glass needle—226. The glass particle was promptly ingested in a typical food cup with a large amount of water. The ameba did not undergo a period of rest but kept on moving forward and in six minutes the glass was excreted—232. It had been completely surrounded by protoplasm. Five minutes later the same piece of glass was again agitated with a glass needle—234. Again the glass was ingested in a typical food cup. Three and one-half minutes later the glass was excreted—237. Another trial with the same piece of glass provoked the formation of a food cup until it was about three-fourths completed, then it was retracted—238. Two further trials produced visible responses, but no complete food cup was formed. The ameba became increasingly indifferent toward the artificial stimulation with each succeeding trial.

Silicic acid.—An A. dubia was stimulated with oscillatoria threads until a food cup was partly formed, then a grain of silicic acid was placed in it and stimulation with the alga filaments resumed—240. The food cup closed up apparently completely, for three minutes after the closing of the cup the silicic acid was actively thrust out as a piece of undigested food material might have been thrown out—244.

Carbon.—A fragment of purified carbon was laid on the back of a raptorial ameba—245. The carbon was raised up by the protoplasm immediately underneath it, but very soon thereafter it rolled down the side of the ameba. A large pseudopod was then sent out over the carbon but no distinctive food cup was formed. When the ameba was forcibly rolled over, it was found that the carbon adhered to the ameba. No attempt had been made to surround it after the psuedopod was laid over it.

Indigotin.—A piece of indigotin was laid in front of an A. dubia and agitated with a glass needle—247. The indigotin was eaten by means of a typical food cup containing a large quantity of water. The ameba moved on in the original direction. Nine minutes after the indigotin was ingested, it was left behind. It is uncertain whether the indigotin had been completely ingested.

The experiments recorded in this section demonstrate conclusively that amebas respond positively to mechanical stimulation. Food objects when mechanically agitated, are more readily eaten than when lying quiet, and in many cases food objects are not eaten at all unless they are in motion. Further, insoluble objects, like glass, are not eaten when lying quiet, but when agitated properly they are readily eaten. It is not necessary for a solid object to come into contact with the ameba in order that a food cup may form; vibrations of the water are quite sufficient to produce the feeding reaction. A chemical stimulus is therefore entirely unnecessary in order to set off the feeding reaction. Movement is not only a contributing factor but it is in itself an efficient factor in calling forth the feeding process.

It will be noted that when vibrated particles are eaten, they are seldom retained for more than a few minutes, whether they are of food value or not. The reason for the speedy excretion of such particles is that the chief, if not the only quality of the particle which incited the feeding process, movement, disappears when the food cup closes, for mechanical vibration is then no longer possible. Since the most attractive quality suddenly disappears, the feeding process stops before it is entirely completed. The formation of a food cup resembles to some extent a reflex act: when an agitated particle of glass is eaten, the formation of the food cup continues for some time after the vibrations have ceased. The formation of food cups is due to a racial habit which is guided to a greater or less extent by circumstances attending the formation of a cup at any particular time. Since circumstances vary greatly, one observes great diversity in the behavior toward particles which produce positive reactions.

Whether the swallowed particle is retained or speedily excreted is largely independent of the character of the feeding reaction. The food cup may have been perfectly formed and yet the particle inciting it may be speedily excreted; or on the other hand, the food cup may have been very imperfect, but the particle may be retained. The retention of a vibrated particle in the ameba seems to depend on qualities other than those which caused ingestion. What such qualities are cannot be definitely stated. The composition of the particle seems to have relatively little to do with it, for food particles like globulin are frequently thrown out at once, while glass is always thrown out; and cholesterin, presumably an indigestible substance, was in one case retained for over and hour and a half. The condition of hunger in the ameba is one of the most important factors. But whatever the factors are which control retention, it is certain that they are not the same as those conditioning ingestion.

DISCUSSION OF EXPERIMENTAL RESULTS

Choice of food.—What is choice? This is a very troublesome concept in science. We need some such word as choice in describing the reactions of animals in order to avoid hopelessly confusing circumlocutions, and yet it seems impossible to give a satisfactory definition of choice from an objective point of view. Since I wish to discuss particularly the phenomena of choice of food in this paper, I shall undertake to explain how I use this word.

Choice has been used to label a process by which a certain state of matter in a system is brought about. More restrictively, it has been used to designate exclusively the end result of such a process, the state of matter after the process has ceased. It is obvious, without illustration, that these two meanings of the word are quite distinct from each other and that they can conveniently be qualified by using, respectively, the phrases " process of " and " result of " choice. The word choice is also sometimes used to describe such processes as, for example, the action of a magnet upon a mixture of sand and iron filings. This is an unfortunate use of the word and two objections may be urged against this usage: first, an equally intelligible description of the action of the magnet can be given without the use of the word choice; second, choice might with equal propriety, be applied to every movement of matter in the universe. It is therefore a hindrance to clear thinking to use the word choice as descriptive or nominative of such processes as these.

Again, the concept of choice is frequently restricted to processes observed in organisms, that is, to conscious processes. This view, although of the greatest interest, is very difficult to consider from our present objective experimental point of view, since it would be necessary first to determine whether an animal whose power of choice is in question, possesses consciousness.

The concept of choice is thus seen to occupy a difficult position in science. If a process in organisms can be described as a sequence of events, we may adopt the view that we do not need the word choice in the description of these events; if, on the other hand, a process of choice cannot be described as a sequence, we cannot from the point of view of objective science use a metaphysical concept—consciousness—as a directive force to explain the phenomenon, but must conclude that some of the events in the chain of sequences are still unknown.

Perhaps the chief objection to the use of the concept of choice is that it insistently calls to mind a *relation* existing between, for example, an ameba and some particles which it senses. The *relation* between the ameba and the particles is made to occupy a more important position in the mind than either the ameba or the particles by themselves. The concept is strongly metaphysical, for the instant one seeks for a relation between phenomena one steps into the borderland of metaphysics. A thousand and one other concepts without which we could not possibly get along in science are just as truly metaphysical, but for various reasons we have fallen into the habit of not noticing this characteristic.

Again, the concept of choice originates almost wholly from subjective material, and in ordinary usage it has first of all a subjective meaning. It is supersaturated with anthropomorphism. Let us say that a man chooses an apple from among some oranges. How would these phenomena be related objectively without connoting a subjective process? A kinematographic record even, without any words at all, would be certain to suggest a subjective process. But although we ordinarily thus think of the subjective process, nevertheless if the same events should be made known to us in a paper on animal or human behavior, we would disregard the subjective meaning and center attention only on the objective phenomena. It is, in short, the meaning we are after and the point of view, not the words merely.

To some investigators of behavior such words as selection, choice, etc., are anathema. They would avoid them as they would the plague. But they themselves do not wholly succeed in avoiding them. How would the idea: The ameba selects its food—be rendered on this view? This idea could conceivably be presented, as in the case of the man selecting an apple from among some oranges, by a kinematograph without the use of a word. But would the general impression on the mind be any different, i.e., would it be devoid of subjective elements? It is just as anthropomorphic to say that the ameba eats globulin and leaves carbon, as to say, the ameba expresses choice between globulin and carbon (eating the former and not the latter).

Briefly then, the word choice serves for two purposes. First, it is used as a hypothesis, as a tool of research. It postulates a certain kind of relation which is to give direction to investigation. All except haphazard investigation proceeds in this manner. Second, its use is indispensable for brief and intelligible description; but any subjective connotation which the word may call forth should be disregarded by the reader unless the author specifies definitely otherwise. It is in this latter sense that the word is used *in the descriptions in this paper.*

In a former paper ('10) I demonstrated that the ciliate stentor is capable of exercising very nice discrimination among the various particles which are carried to its mouth by its cilia. Not only is the discrimination between food and indigestible particles (excepting carmine) very precise, but even among food particles themselves, certain organisms being eaten and others rejected. This is particularly noticeable when the stentors are partially satiated.

Now ameba discriminates with equal or perhaps greater precision. Excepting carmine, no indigestible substances are eaten unless agitated. Of the various things eaten, living organisms, such as flagellates, coleps, etc., come first in point of preference. Then comes globulin, grain gluten, carmine, and tyrosin. Less attractive than these are: aleuronat, fibrin, lactalbumin, ovalbumin and keratin, and peptone in solution. Digestible substances that are eaten only occasionally are soluble egg white, solid egg white, uric acid. No starch, lecithin, silicic acid, carbon (excepting in one case), sodium chloride, iron, cholesterin, etc., were eaten unless agitated. Sand grains were never eaten under my observation, and I have never seen " numerous " sand grains inside of amebas from wild or laboratory cultures. It will be recalled that sand grains are frequently referred to in text books and elsewhere as " typical " contents of the ameba's body.

How can these preferences be explained? As far as can be told at present there is no single quality possessed by all the substances which ameba eats, which might be looked upon as the basis of selection; nor do the refused substances possess a common quality which causes amebas to leave these substances alone.

Excepting carmine, all the substances which ameba readily eats are (presumably) digestible, though only two were actually tested in this respect: globulin and grain gluten. But a number of substances which are digestible, such as for example gelatin, egg albumin, fibrin, etc., are eaten only very occasionally or not at all. Of the lifeless solid substances, those which are the more soluble (excepting gelatin and egg albumin, which are very soluble, and globulin which is said to be insoluble) were the more readily eaten. But it is possible that in the case of globulin impurities were present, or that the salts in the water caused slight solubility. The attractiveness of carmine and of lead oxide, and the general indifference toward zein, fibrin, keratin, etc., might be due to the solubility of the former and the insolubility of the latter. Tyrosin is the only rapidly dissolving substance eaten. It is very attractive, but it seems that its rapid rate of solubility is slightly disagreeable or injurious. But there are still several items of behavior that cannot be explained even if an essential part of the basis of selection among lifeless substances should be the rate of solubility. Thus, why should the soluble proteins: egg albumin and gelatin, be passed by with indifference? Or what explanation could be assigned for the fact that solids such as tyrosin and carmine call forth feeding reactions very readily when these substances are in the actual process of dissolving, but if a capillary tube filled with solutions of these substances, is presented, the feeding reaction is not produced? It is clear that neither solubility as such nor the rate of solubility determines in all cases whether a lifeless substance shall be eaten or rejected.

The opinion has become quite general that the chemical constitution of substances determines whether an animal will eat them or not. This view, however, has no experimental support; but on account of its general acceptance, especially as applying to unicellular forms, it may be profitable to examine it in some detail.

Just how can a substance affect a sense organ? Apparently only in two general ways: its molecules or ions may combine chemically, temporarily or permanently, with a part of the sense organ; or, some sort of physical energy radially propagated from the sensed particles may produce physical changes in the sense organ. If a substance affects a sense organ by uniting with it chemically, such sensations as might result therefrom should be related in some way with the chemical constitution of the substance, and the sensations should vary in some way as the composition of the stimulating substance varies. Such a sense organ would mediate true chemical sensations. It would seem that all the elements of at least a few compounds should be represented in consciousness, by a chemical sense organ, when they are tasted or smelled. But this never happens in man. The taste or smell of a substance of a given concentration, on homogeneous sense organs, is always a simple sensation, such as proceeds from a simple stimulus. There is no evidence from the psychological side, as it is recognized that there is none on the physiological, that organs of taste or smell sense the chemical composition of substances. But on the other hand, there is some evidence that physical qualities are sensed by the distinctive organs of taste and smell as is shown by the possibility of stimulating the taste buds by electricity so that there are produced sensations of sweetness, acidity, etc., depending upon the particular buds stimulated. It is possible therefore to stimulate a sense organ of taste by means of chemicals in solution as well as by electricity, a physical stimulus. But the effect of a chemical on a sense organ is not at all the same thing as a chemical effect on a sense organ.

But this distinction is not always clearly drawn.

Metalnikow, in his very interesting and extensive paper on the feeding habits of paramecium, as an important example, does not make very clear the distinction between reactions to physical and to chemical qualities, although he asserts that the chemical nature of a substance determines whether it will be eaten by paramecium. Let us therefore examine the experimental results and arguments of Metalnikow, in the light of what was said in the preceding paragraphs, to see whether he is justified in stating that paramecium selects its food upon a chemical basis.

Paramecia eat powdered glass, sulphur, chalk, aluminum, sepia, as well as egg yolk, milk, olive oil, and other digestible substances (see p. 398, table 1.), but he says:

> Toutes ces expériences nous montrent avec certitude que l'absorption par les Infusoires des corpuscles suspendus dans l'eau et la formation des vacuoles digestives dépend de la nature chimique de la substance dont sont formés ces corpuscles. Sans aucun doute les Infusoires sont capables de distinguer les différentes sortes de nourriture qui peuvent se trouver à leur portée.
>
> Il est intéressant de vérifier à present si les infusoires peuvent absorber les différentes substances toxiques insolubles dans l'eau. A cet effet, les Infusoires ont été nourris de différents sels insolubles de mercure et d'arsenic, et j'ai été étonné de voir que ces sels sont assez vite absorbes par les infusoires qui arrivent même à former quelques vacuoles digestives; ces infusoires perissent ensuite bientôt. Mais il ne faut pas oublier qui même l'homme et les animaux supérieurs ne sont pas toujours capables de distinguer les substances toxiques, si ces substances sont dépourvues de mauvais goût (pp. 401–402).

It is evident that Metalnikow speaks here of selection by the feeding mechanism, and not of histonic selection, that is by the digestive mechanism of the tissues.

It is difficult to see how paramecia can be said to distinguish between substances on a chemical basis when indigestible and insoluble substances as well as digestible and soluble, are eaten to about the same extent.

Choice based upon chemical qualities is qualitative; each chemical substance must be conceived of as acting specifically. According to this conception, when the sense organ is stimulated the quality of the sensation is exactly expressible; it cannot vary excepting as to its amplitude or continuance. There can be no doubt as to the exact nature of the stimulating object. We would therefore expect an animal capable of choosing on this basis, to choose with great precision. We would certainly expect much more precise selection even if the power of selection was very crude, than is shown in Metalnikow's first table. For according to this table glass and sulfur are eaten apparently as readily as milk or starch and eighty per cent as freely as olive oil (table 1, culture C).

Organismal selection in paramecium seems therefore to be extremely crude; in fact it can hardly be said to exist at all under ordinary conditions.

But even if paramecium discriminated between digestible and indigestible substances, the supposition that it did so on a chemical basis is open to question. For it is assuming a great deal when it is said that paramecium becomes aware in some way of the diverse chemical structure of starch, milk, various bacteria and bacilli, leukocytes, yeast cells, egg yolk, olive oil, albumins, etc., while these substances are passed back to the mouth by the cilia of the gullet. Now in order that paramecium may become aware of the chemical nature of these several substances, new compounds must be formed in the sense organs of the paramecium (the cilia?) involving a permanent or temporary union of a part or the whole of the molecule of starch, albumin, oil, etc., with some structure in the sense organ, to form, in each case, a definite and characteristic compound which would then serve in some way to set into operation the ingesting mechanism. What the chemical equipment of a sense organ would have to be in order that compounds might be thus formed with all the different substances which paramecium eats, it is difficult to conceive. Metalnikow does not attempt to give an explanation of how selection on a chemical basis might operate; nor to my knowledge do any of the other writers on protozoa, although several refer more or less casually to the selection of food as based on its chemical nature. That it is unnecessary to explain choice of food upon a chemical basis in paramecium or in any of the other protozoa whose feeding habits have thus far been investigated, will be shown by examining the process of selection in ameba.

Recently Lund ('14) published an important paper on the feeding reactions of the large ciliate, bursaria. In this paper Lund discusses the selection of food in bursaria, especially as to whether it rests on a chemical or on a physical basis, and in this connection refers to a previous paper of mine treating of similar questions about the feeding behavior of stentor. It seems however, that Lund did not quite understand my conception of the difference between selection of food on a chemical basis and on a physical basis, doubtless because I did not go into the details of the difference as I conceive it. I have examined his paper carefully but, although he insists that bursaria selects its food on a chemical basis, I have nowhere found a discussion in his paper which sets forth just what he conceives to be a chemical basis as distinguished from a physical, in so far as the selection of food is concerned. I have, therefore, found it of interest to examine his paper in some detail, for it is absolutely essential that the difference between selection on a chemical and on a physical basis be clearly drawn, before we can say that an animal selects its food on either basis.

Lund fed bursaria with yolk of hen's eggs untreated, and stained with various chemicals, employing essentially the methods I used in my work on stentor ('10), and Metalnikow ('12), on paramecium.

Yolk treated with various dyes is eaten less readily than untreated yolk. If NaOH, HCl, saffranin, etc., are added to the culture solutions in varying quantities, the yolk is eaten in decreasing quantity in proportion as the toxic substance is increased in concentration. Temperature also has a similar effect; with a rise of temperature from 0° to 35° C., there is a corresponding increase in the amount of yolk eaten. Beyond 35° C. the temperature becomes injurious. In addition to these experiments, Lund mentions some observations to the effect that carmine, india ink, aluminium, carbon black, cinnibar, etc., are eaten by bursaria (p. 43).

It appears then that bursaria stands between stentor and paramecium (and close to paramecium) as far as concerns its capacity to discriminate in feeding.

From the results of his experiments, Lund expresses agreement with Metalnikow ('12) in so far as the basis of selection is concerned.

But it was shown in the preceding pages that Metalnikow's conclusion that food is selected on a chemical basis is not in agreement with all the facts; and the same criticism to which Metalnikow's conclusions are open, also apply to Lund's. It will therefore not be necessary to go over this ground again. It should be noted however, in this connection that Lund dismisses with a single paragraph, as if they did not bear at all on the question of selection, all the observations he made on the eating of chemically inert substances, such as aluminium, carbon, etc. But it is precisely these observations which most strikingly contradict his notion that selection is made on the basis of the chemical composition of the substances. *How can* *one explain the selection of insoluble substances such as carbon or aluminium, which are eaten, on a chemical basis?*

The experimental results which form the basis of Lund's conclusion admit of another interpretation. The fact that more and more yolk was eaten as less and less of NaOH, HCl, saffranin, etc., was present, does not of course indicate active selection; the presence of toxic substances affected the general bodily condition so that feeding was to some extent suspended. It cannot be inferred that the bursarias "tasted" with the food selective mechanism the toxic substance, and on this account refused to eat less as this substance was more and more concentrated. The experiments with temperature show a feeding gradient that corresponds almost exactly with that obtained in those experiments where toxic substances were employed in varying concentrations. Clearly therefore, there must be other evidence to show that selection is based on chemical constitution; for the observation that chemicals in varying concentrations prevent feeding to a greater or less extent, does not mean that these chemicals were 'tasted' by the mechanism of food selection any more than that the various temperatures, or the electric current, or the mechanical stirring, were tasted. In other words, the feeding mechanism in bursaria, as in many other animals, is affected by stimuli affecting the general bodily condition, as seems to be the case when stimulated by agitating mechanically the medium in which the bursarias live, or by passing electric currents through the medium, etc. In these cases the inhibiting impulses arise in other parts of the body, and are transmitted to the feeding mechanism.

Chemical solutions, when mixed with the medium, also affect the sense organs of the ectoplasm generally, so that feeding may be inhibited without involving the action of the food selective mechanism at all (see Lund, pp. 41, 42). Whether Lund succeeded in localizing the effect of stains absorbed by the yolk grains so that only the food selective mechanism was affected and then not injuriously, is very doubtful; that he did succeed may not be concluded from his experimental results. It is probably superfluous to add that unless one is sure that the food selective mechanism is at any time regulating the feeding mechanism, discussion of the bases of food selection is beside the point.

The distinction between the feeding and the selective mechanisms is not merely academic. The distinction can readily be made in the higher animals, and there are some observations in my paper, viz., those where tyrosin was fed, which show that the distinction is experimentally verifiable in ameba. But the clearest illustration of this point among the lower forms is to be found in stentor.

It follows, then, that those experiments where various temperatures, electric currents, toxic substances, were employed, important as they are of course from other points of view, cannot be admitted as evidence in support of the chemical theory of food selection. And as to those experiments where the yolk was stained and the superfluous dye washed out, it is really doubtful if there is evidence here that bears on the problem of choice of food. The adsorbed dye gradually washed out, according to Lund, in the course of the experiments, and it is, therefore, next to impossible to be sure that only the food selective mechanism is stimulated when a response is obtained; but this, as has been said, is the first essential in investigations on choice of food.

The food selective mechanism is the most delicate mechanism affected by food substances, and it is the last mechanism that tests the particle before it is eaten or rejected. A particle of any substance must not cause a general negative reaction before it affects the food selective mechanism, otherwise the animal cannot express choice as to its food qualities. If the body reacts negatively to a particle (solid or in solution) before the food selective mechanism is affected, the result is choice only between indifferent and injurious substances. That is to say, an injurious substance produces a negative reaction, while all other substances are indifferent. The presence or absence of food qualities is not the basis upon which choice is made under such conditions. As a concrete case we may refer to Stentor caeruleus. So far as we know, the cilia of the disk of stentor are not a part of the food selective mechanism. But they are a part of the feeding mechanism. Food materials, carmine, starch grains, glass, sulphur, etc., brought to the disk by the vortex produced by the membranellae, are all transferred to the pouch and funnel leading to the mouth. But when an injurious substance comes into contact with the disk, a negative reaction sets in. The discal cilia accept indifferent or non-injurious particles and reject injurious substances. But when the particles reach the pouch and funnel, selection is made on a different basis, for here starch, glass and sulphur are rejected, while food particles are eaten. When injurious substances affect the disk feeding is for a longer or a shorter time more or less completely inhibited. The decrease in the amount of food eaten in such a case is not due to activity of the food selective mechanism, for the stimulus resulting in partial or complete cessation of feeding arose in another part of the organism where selection between food and other materials has been shown not to occur. It seems then that choice of food such as is observed for example in stentor and in ameba results from the presence in particles of qualities which *induce* feeding, and not from the presence in other than food particles of qualities which *prevent* the ingestion of these particles.

In so far as selection is concerned, all of Lund's experiments, including those where carmine, cinnibar, carbon and other indigestible substances were eaten, can be explained by assuming that choice is based upon the physical properties of the substances, and that all solid non-injurious particles of handleable size are eaten. But if toxic substances are present, or if the temperature is too low, or if an electric current is present, or if the bursarias are violently agitated, the bursarias are disturbed or injured and not only choice but feeding is suspended to a degree corresponding to the strength of the stimulating agent. This simple explanation covers all the recorded facts of feeding in bursaria, and conforms with the explanation of the selective processes in stentor and paramecium, and to a considerable extent with that of ameba.

It has already been pointed out in several places that A. dubia is readily stimulated by moving objects; and that almost any object in vibratory motion is eaten, whether the particle is composed of glass or carbon, or whether it is a living or a dead organism. So ready is the response of these amebas to objects in motion, that their seldom reaction to motionless objects, or to lifeless objects, is readily overlooked. Thus Gibbs and Dellinger ('08) whose plates II and III indicate that they probably worked with this species, concluded that "Amoeba eats nothing dead."

"The Amoeba shows distinct food preferences; with diatoms and unicellular algae, it takes algae, but when feeding on algae it will leave them to " pursue " ciliates. In the presence of large paramecia, some amoebas leave algae and ciliates to catch these larger forms. Amoeba eats nothing dead. This was observed in the case of dead diatoms and algae cells, of paramecia dead from natural causes, and of paramecia which had been artificially killed. Amoebas do not apparently eat their own species, but were seen to eat amoebas of other species " (p. 240).

As we have seen, however, A. dubia eats lifeless things, though only very rarely (see under carmine, Schaeffer, '16a, '16b under " raptorial " amebas). My observations confirm theirs on reactions toward dead organisms or parts of organisms: none are eaten. Now when it is remembered that in the normal life of an ameba neither carmine nor isolated proteins occur, it is clear that movement in an object is practically the only quality which induces feeding in A. dubia. In other words we have conclusive proof that the chemical nature of the moving eaten object is of no importance whatever in so far as feeding is concerned, and that the quality that actually determines ingestion is clearly a physical quality. The ability to discriminate among substances on a chemical basis while feeding, might, therefore, be entirely absent in A. dubia without affecting its ability to live successfully.

So far as normal feeding is concerned, A. proteus has practically the same habits as A. dubia, in that by far the larger quantity of food consists of living moving organisms, which are selected because of their movement. But it differs from A. dubia in that dead organisms and fragments of isolated proteins, etc., are readily eaten. Here, manifestly, selection is made upon a broader basis. But if all the experiments where motionless objects are eaten are taken together it does not seem possible as we have already seen that choice based upon a single factor could lead to such diversified behavior. Thus if the chemical nature of substances stimulated ingestion (1) carmine would probably not be eaten; (2) solid and soluble egg albumin and gelatin would probably be eaten with avidity; (3) globulin, lactalbumin, ovalbumin, which are said to be insoluble, would be eaten; (4) uric acid would not be eaten; (5) capillary tubes filled with carmine solution and with tyrosin solution would be as attractive as solid carmine and tyrosin respectively; (6) food cups would be formed when the chemical substance was first sensed, instead of after the source of diffusion was reached. Then there is the further general observation that the ameba moves directly toward a stimulating object, if positively attracted. That is, the ameba moves parallel with lines of diffusion radiating from the soluble object; or, if the object is not soluble, along lines of force of another nature propagated in a similar manner. It is clear therefore that for lifeless objects, choice cannot be based on a single factor, nor can it be based exclusively on the chemical composition of the sensed objects.

The ameba seems to be stimulated at several points by a sensed object, and locomotion then proceeds along the line of intensest stimulation. This is a method of reaction directly comparable to that of the higher animals, when stimulated positively by heat from a definite source. The whole ectoplasm (particularly the anterior portion) may be considered as a sense organ capable of receiving stimuli at many points with local reference. That the stimulus itself (for example, a change of surface tension) directly conditions the path of movement seems impossible; for the nature of the responses to stimuli is not at all machine-like, as the experiments abundantly show, and as they would necessarily be if the stimulus directly determined the reaction.

One of the chief difficulties in the way of accepting the hypothesis that food is selected on a chemical basis is the discovery that organismal and histonic selection are not synonymous. This is very significant. Carmine, which is invariably readily eaten, is nevertheless always speedily egested. It seems to make little difference whether the ameba is hungry or nearly satiated, speedy egestion follows the ready eating of carmine. Similar, though not as striking results, are obtained in the behavior of A. dubia toward lactalbumin, uric acid, etc.

Now, if the chemical nature of an object is thoroughly tested at any time by an animal, it is just after it is eaten. The digestive juices then begin to act upon it chemically, and its constitution then determines what will happen to it. In a general way, if the substance is digestible and harmless, it remains in the body; but if indigestible or irritating, it is soon excreted. Now the fact that organismal selection, in many cases, leads to results directly opposed to those of histonic selection, demonstrates conclusively that these two methods of selection do not rest upon the same basis.

Although Metalnikow did not seem to recognize the difference between organismal selection (exercised while feeding) and histonic selection (exercised when the process of digestion begins), his data clearly indicate that carmine, aluminium, powdered glass, sulphur, etc., are as readily eaten as, but more speedily ejected than food particles. The fixed habit of cyclosis in paramecium, and that of egestion at a definite point, serve to obscure this difference somewhat, for it tends to equalize the time during which digestible and indigestible substances are retained in the body. But the fact nevertheless stands out when Metalnikow's tables are closely examined. Thus if tables I and IV are compared, it is observed (table I, culture C) that glass and sulphur are eaten more readily than milk, as readily as starch, and nearly as readily as olive oil; while table IV shows that (in other cultures, it is true) these substances are excreted much sooner than starch, olive oil, or milk. It is quite evident, then, that the ectoplasmic evaluation of substances differs from the endoplasmic, in paramecium as distinctly as in ameba, though not as strikingly, and that choice of food is not made upon the same basis by the ectoplasm and the endoplasm.

Seeing then that organismal selection of food as observed in ameba is not explicable on a chemical basis, one naturally looks to physical properties for the explanation. Is selection based upon physical properties? Unfortunately a complete answer is not yet possible, nevertheless we may consider briefly the direction an explanation of selection on a physical basis would take.

It is not necessary to suppose, in the first place, that each substance to which ameba reacts, stimulates the ameba in a specific way. It is possible that many of the substances as sensed differ from each other only quantitatively in certain physical characteristics. This is, for example, the case in man with most tasting substances. The various sugars and saccharin differ from each other only quantitatively in taste, supposing that the taste buds for sweetness only are stimulated. The same is true for various acids. And as a further illustration one may refer to color vision. Here a large number of quantitatively varying ether vibrations produce specific sensations which are then qualitatively interpreted. Attention may also be called to the fact that man does not acquire a knowledge of the chemical composition of any single substance directly by a sense organ. The nearest approach to obtaining such knowledge is in the smell sensations of the elements chlorine, bromine and iodine; but even with these substances it has been pointed out that the mucous membrane, aside from the olfactory nerve endings, may be stimulated, and that nascent hydrogen may combine with these elements before the sense organ is stimulated. We cannot conclude, therefore, that iodine, bromine and chlorine are sensed in the elemental condition. Now since we do not find any conclusive evidence in man (or elsewhere) that the chemical composition of substances is sensed, not even in a single case, one must, to say the least, feel suspicious of the correctness of the chemical hypothesis. Differences in surface tension, adsorption, rate and direction of diffusion of dissolved molecules, ionization, reflection of light from suspended particles, etc., are probably among the properties which play a part in determining the feeding behavior of ameba. The disturbance due to moving animals in water, which is transmitted as waves of changes of pressure to the ameba, and which, as we have seen, is the most potent stimulus for setting off the feeding reaction, is purely a physical property, and it is not unlikely that the effect of the pressure waves is a change in the distribution of surface energy on the part of the ameba affected. While we are far from explaining all the acts of selection in ameba on a physical basis, a respectable beginning has nevertheless been made, as we have seen in the section devoted to the effect of mechanical agitation.

What has been said about the basis of selection in this section has had reference only to individual acts of selection; the eating of a grain of carmine or of globulin, or the avoidance of a grain of carbon, each taken by itself. A very important element affecting selection in a broader sense, that is, selection as the sum of the feeding behavior of an ameba, has not yet been mentioned. This element is the effect of previous experience.

The importance of this factor in selection is equalled by the variety of ways in which it may express itself. The previous stimulus and response characteristically affects the succeeding response. In some cases the effect is slight compared with the stimulus; in others the effect of the previous stimulus and response is much more important than the succeeding stimulus. Thus in experiments 6–13 (Schaeffer, 1916c) the sensing of tyrosin grains affected the ameba in such a way that the succeeding grain of globulin was treated at first like a grain of tyrosin. But after the ingestion of the globulin, the succeeding grain of tyrosin was treated like the grain of globulin, and promptly eaten. The behavior of the ameba was ordered with definite reference to its past. It is clear that each of these items of behavior, taken by itself, could not be explained. The process of selection cannot be understood by treating in a quantitative manner a number of separate acts of choice. On the contrary, selection must be looked upon as a *connected, developing process involving at least the entire past of the individual ameba.*

SELECTION OF FOOD IN STENTOR AND PARAMECIUM AS COMPARED WITH THAT IN AMEBA

In this section are summarized the chief facts bearing especially on the selection of food in stentor, paramecium and ameba. A comparison of the main results of investigations on these organisms serves to give a better conception of this problem of choice of food, I believe, than can be had in any other way. Incidentally, such a comparative study gives also a hint as to the probable path of development in a species of whatever method of selection may be present in that species. The reason for selecting these three organisms is that they serve as types of three methods of selection, and what is equally important, the food selective processes are better known in these three organisms than in any other lower forms.

Paramecium. Paramecium feeds on bacteria and other very small particles, but bacteria form much the larger part of the normal diet.

A very great number of particles, hundreds of thousands or millions, must be eaten every day in order to maintain life.

If the particles were tested individually, an enormous amount of time would be consumed in the process, and there would not be sufficient time to eat the optimal amount of food. The ingestion of particles of sand, debris, mud, silt, etc., if each particle were tested individually, could therefore not be considered an advantageous reaction, since it would entail a dangerous decrease in the amount of food eaten. In times of very slightly muddy water, paramecia would starve to death if careful selection should be practiced, for the time consumed in rejecting silt would permit but very little food to be eaten. It is therefore of advantage to paramecium not to examine finely divided particles individually, since the maximum amount of food can be obtained under normal conditions without selection, and the few particles not of food value that may be ingested are harmless.

It may be supposed then that paramecium has lost the power to a greater or less degree, of selecting its food as it is brought to its mouth. Everything that is finely divided is eaten, whether poisonous or not. Metalnikow's experiments ('12) where powdered glass, sulphur, aluminium, arsenic salts, etc., were eaten, prove this point very strikingly. The physical quality of solidity of a substance is sufficient to set off the ingesting mechanism, provided the particle is of such size that paramecium can take it down the gullet.

The positive responses of paramecium to many chemicals, as worked out by Jennings and others, may be interpreted as a reaction to a stimulus which has become associated with the presence of food, most of these chemicals probably stimulating paramecium in a manner similar to carbon dioxide, which is always found where bacteria are found, and with which paramecium continually comes into contact. It is not necessary to suppose that each of the positively stimulating chemicals has a characteristic stimulus. The reactions do not indicate this, and it is quite an adequate explanation to assume that the sensation is the same in quality for most or all of the chemicals in solution producing positive behavior. The intensity of the sensation may vary, however, for different substances, as it seems to vary with the degree of concentration of any one of certain chemicals. The fact that paramecium reacts to chemicals does not at all indicate that the composition of the chemical substance is sensed by the paramecium, or even that a qualitatively characteristic response is produced in the sense organs by each substance. It is likely that some physical property, common to carbon dioxide and to other substances causing positive behavior, stimulates the paramecium. There are a number of instances in which it has been definitely shown that a physical quality of an object stimulates amebas, stentors and paramecia, but there is no case where it has been definitely shown that a characteristic response is due to some chemical effect. The reactions of paramecium, therefore, can be consistently and adequately explained by assuming that physical qualities act as the stimuli.

It remains to mention that selection of food is accomplished roughly by the avoiding reaction. If a paramecium comes to a locality where an injurious chemical is dissolved in the water, the paramecium avoids the locality and all solid particles in it. If, however, an attractive chemical such as carbon dioxide is present, the paramecium enters the water where the diffused chemical is and eats all the particles of proper size there without expressing any choice among them, for carbon dioxide is not injurious in dilute solutions. Inside of the funnel or gullet of paramecium there is practically no selection, though Metalnikow has shown that the power to discriminate may be developed very appreciably by proper experimentation (Metalnikow, '12).

Stentor caeruleus. The blue stentor feeds on small particles such as bacteria, and also on larger forms such as ciliates, flagellates, rotifers, zoospores, unicellular algae, etc. It is difficult to say what the normal diet of stentor is, but it may be mentioned that laboratory cultures can be raised very successfully on bacteria and flagellates such as chilomonas. The number of particles eaten per day depends of course upon the size of the particles. Ten paramecia may be quite sufficient, but it would require thousands of flagellates and millions of bacteria, if either of these kinds of organisms were eaten exclusively.

Stentor has a food sorting mechanism by means of which any particle can be ingested or rejected 'at will.' The selective mechanism acts with great precision, especially when the particles are of appreciable size. In such case relatively few particles need to be eaten to maintain life, and there is consequently sufficient time for careful selection of individual particles.

It is reasonable to suppose that it is advantageous to stentor to sort out the food particles from all that are brought to it, whenever these particles are of large size.

Stentor still possesses the power to choose its food especially where larger particles are concerned. But indigestible material may be eaten when very hungry. Very small grains of indigestible material (carmine) are refused to a much greater extent when food is present than when absent. Large particles of glass, sulphur, starch, are consistently refused.

The experimental evidence makes it highly probable that selection is based upon the physical (tactual) properties of the substances (Schaeffer, '10).

As compared with paramecium it is true that stentor is capable of much nicer discrimination in the laboratory tests, but it is probable that in natural surroundings the methods of paramecium in food selection are quite as well fitted as stentor's for successful living, if not more so.

Amoeba proteus, *A. dubia*, *A. discoides*. Ameba feeds on large solid particles, living or dead; protozoa, protophyta, rotifers, zoospores, masses of zooglea, dead masses of protoplasm, etc. Whether ameba takes in liquid food is not known.

Usually only one or two particles are eaten at a time. Several particles of such forms as urocentrum, paramecium, desmids, may be sufficient for a day's feeding; or if the organisms are small, such as chilomonas, several hundred are eaten. There is therefore sufficient time for selection in every case.

Ameba eats normally only digestible matter. The degree of precision of selection in ameba compares favorably with that in stentor.

Ameba still possesses the power of selecting its food.

Selection is based, in many cases, upon the physical properties of objects such as, for example, movement.

Ameba rejects an undesirable object by moving away after coming into contact with it; or by not moving toward it if the stimulus, such as very violent movement, is too intense.

Comparing the processes of choice in food in these three protozoans, we observe that in paramecium an enormous number of particles must be eaten daily to sustain life, so many particles in fact that a process of selection could not be applied to each individual particle. And experiment shows that selection of food is almost completely suspended in this organism. Stentor feeds on large particles as well as on small ones, such as bacteria. Stentor can live readily on a few large particles eaten daily, and there is abundant time for careful discrimination. Experiment shows that stentor is capable of very nice discrimination. Ameba eats only large particles and in this organism also very nice discrimination is exercised. In all these protozoans selection is based upon physical characters of the food objects rather than upon their chemical constitution. Thus, among amebas, movement of an object is in a very large number of cases an adequate stimulus; stentors seem to react to a composite stimulus formed of several qualities such as weight, surface texture, shape, size, solubility, etc.; while paramecia seem to be sufficiently stimulated by the solidity of particles of small size.

Not only has the extension of the sensing range of food objects been based on the physical characters in these protozoa, but also in most if not all of the higher animals as well. Thus all seeing animals depend more or less on the physical characters of objects as a basis for choosing their food. After objects are selected by sight as suitable for food, another test is made of them by the sense of taste, or touch, or smell, or all of them together. But there is at least one group of animals that depend on sight almost, if not quite exclusively—the anura. Only moving objects are snapped up, and these are usually snapped up with such vigor that even if they are found disagreeable in the mouth, such as hairy caterpillars are, for example, they often cannot be ejected. A frog would starve in the presence of motionless food objects. It is likely also that in many seed eating birds, taste and smell play a very minor part in food discrimination. There has, in short, been a tendency in animals generally to increase their sensing range of food by reacting to distinctive physical qualities, especially such as can be sensed at a distance, until in some forms, according to experimental evidence, none but physical qualities are concerned in selection.

SUMMARY

1. Ameba is capable of exercising very nice discrimination in feeding between two particles of different composition—one digestible, the other not—lying very close together. When the particles stick together slightly, the food cup in some way separates them so that the food particle comes to lie inside the food cup while the other particle is actively pushed to the outside. The ameba not only expresses choice between particles of different composition under special conditions therefore, but if the conditions are such that a choice cannot at once be made, the ameba can change the conditions (separate the particles) so that a choice may then be made.

2. The experiments with two particles of diverse composition

indicate, in conformity with the results recorded in my previous papers, that some physical disturbance propagated radially from the source of stimulation is an essential factor in determining the direction of movement of the ameba.

3. No definite statement can be made regarding the basis upon which choice in general is made. In a general way only digestible substances are eaten, but some digestible substances are refused (zein, gelatin) and some indigestible substances (carmine, india ink) are readily eaten. It can be stated however, that the basis of selection is not chemical in any known case and that in several important cases selection is based upon physical properties.

4. Movement of a particle is one of the most important, if not the most important food quality a particle can possess. Particles of glass, which are never eaten when lying still, are readily eaten when agitated.

5. The experiments with mechanically agitated particles bring out very strikingly the difference between organismal and histonic selection. The ingesting and the digesting mechanisms differ profoundly as to the food value of a particle of agitated glass, for example.

6. Observation and experiment indicate that amebas might possibly be able to exist and propagate indefinitely in nature if they selected their food on the basis of movement alone.

7. The experiments show that, in many cases, past experience in receiving stimuli or in feeding is of more importance in selection than the nature of the stimuli received from a present object.

Many individual acts of selection cannot therefore be explained when standing alone, but only when the ameba's past, especially its immediate past, is known. Selection is therefore a historical process. The main factors, then, that enter into selection are physical and experiential.

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EXPLANATION OF PLATES

The figures are camera lucida drawings of sample experiments taken from the laboratory notes without alterations. The camera lucida was attached to the long arm of a Zeiss binocular microscope. Eyepiece 4 and objective a_3 were used, giving a magnification of 65 diameters. A scale by means of which the size of amebas and of test objects can be estimated is shown on plate 4.

The figures are numbered serially from 1 on for reference. These numbers are placed inside the figures. They are to be looked upon as labels only. They have no other significance. An x following a number, as 13x, indicates the end of the experiment illustrated by figures 1 to 13 inclusive. A new experiment starts with figure 14 and ends with figure 25x, and so on. A number followed by xx indicates that the next experiment was performed upon a different ameba. Thus figures 1 to 66xx represents the results of a number of experiments upon the same ameba. With figure 67 a new ameba was employed, and so on. The order in which the figures were drawn is represented by the serial numbers for all the figures in any one experiment, and in nearly every case for all the experiments performed on any one ameba.

The time of the beginning and the end of each experiment is given in hours and minutes. In some cases the time of drawing of each figure is also given, and where it is not given it may easily be computed.

The arrows show the direction of active protoplasmic streaming. The arrows in the last figure of each experiment denote the direction the ameba took in moving away from the test object.

The test objects are labeled in abbreviated form. See table of abbreviations below. For quick and correct reference the test objects are connected with the proper amebas by leader lines. These lines have no other significance.

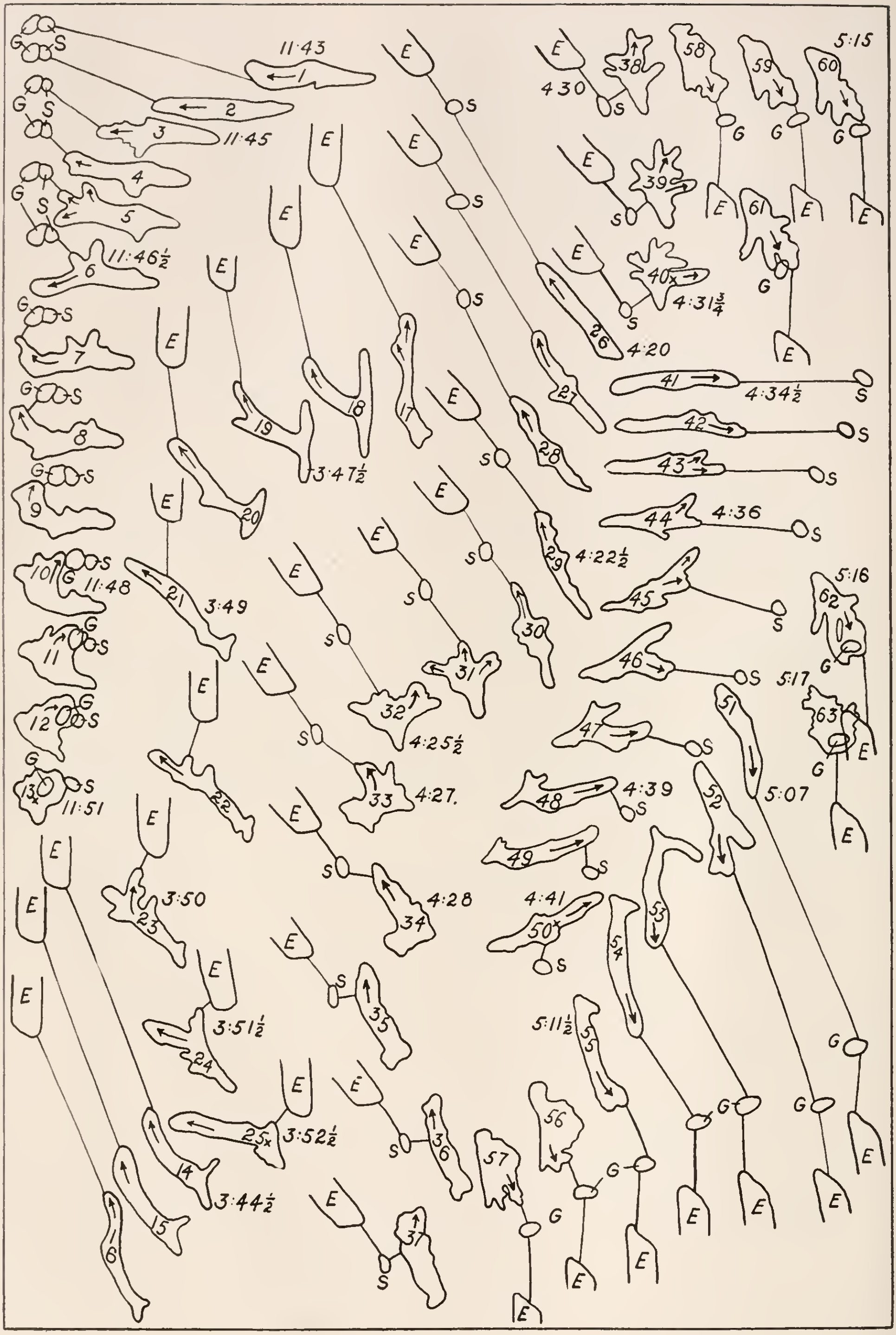
All the work was done facing a north window. All the figures were drawn in the same position in the laboratory and on the plates. The top of each plate therefore points toward the north. This is worth noting from the point of view of the possible influence of light on the behavior of ameba.

It will be noted that there are slight differences in the size and shape of the same test object as drawn in the figures of any single experiment, even if the object was not rolled around by the ameba. The explanation for these differences lies in the speed with which the drawings had to be made in order to catch important items of behavior. As a rule the parts of the ameba lying nearest the test object received the most careful attention and were drawn first; the posterior parts of the ameba and the test object were drawn last.

For detailed explanation of figures see pages 221 to 231 of the text.

TABLE OF ABBREVIATIONS

AM,	ameba	GG,	grain gluten
CA,	carbon	GL,	glass
COL,	coleps	H,	hematin
E,	egg albumin	IN,	indigotin
F,	fibrin	LE,	lecithin
FC,	food cup	S,	silicic acid
G,	globulin	U,	uric acid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3:52½
4:20
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4:28
4 30
4:31¾
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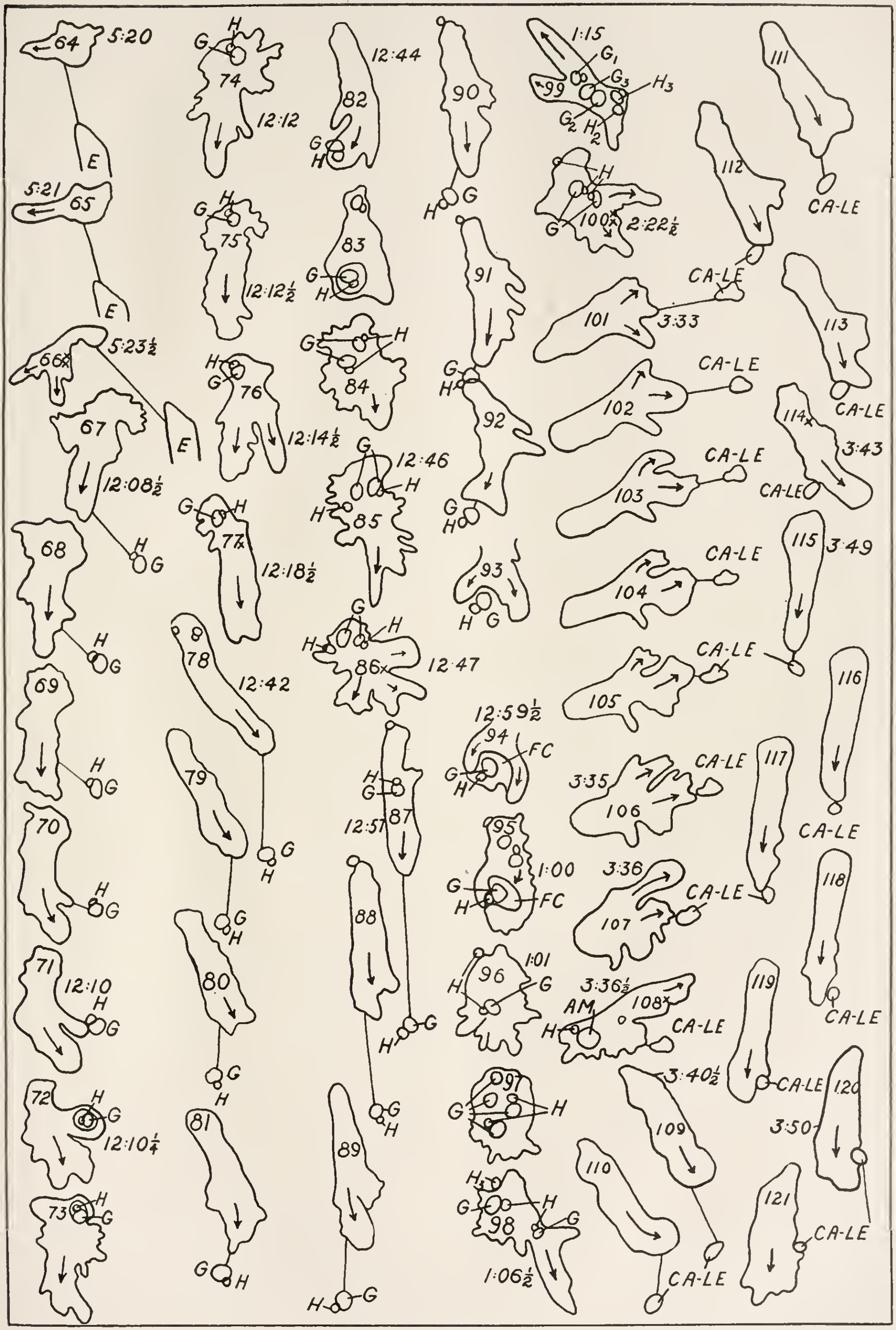
5:17

Figures 1—63.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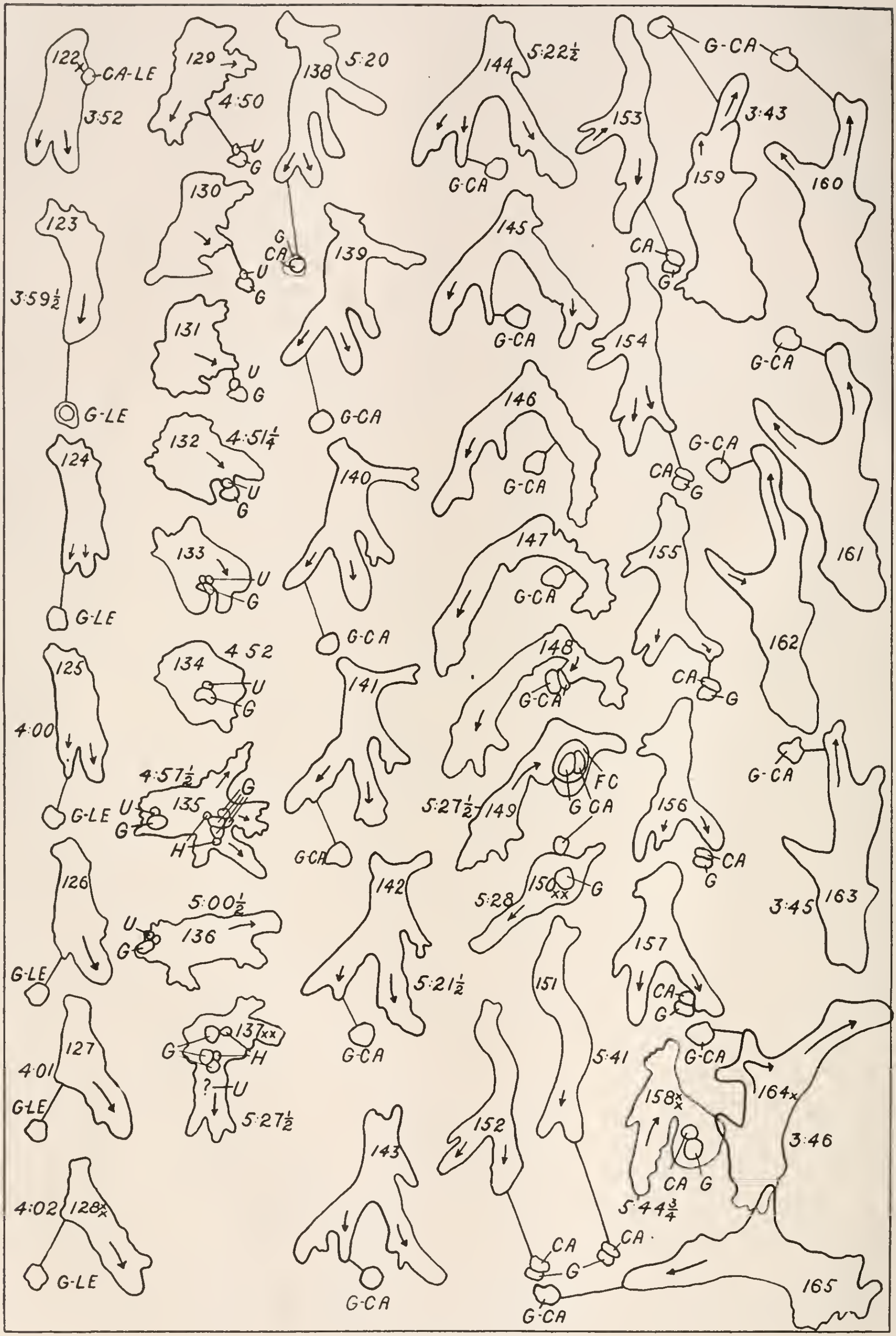
121
CA-LE

Figures 64—121.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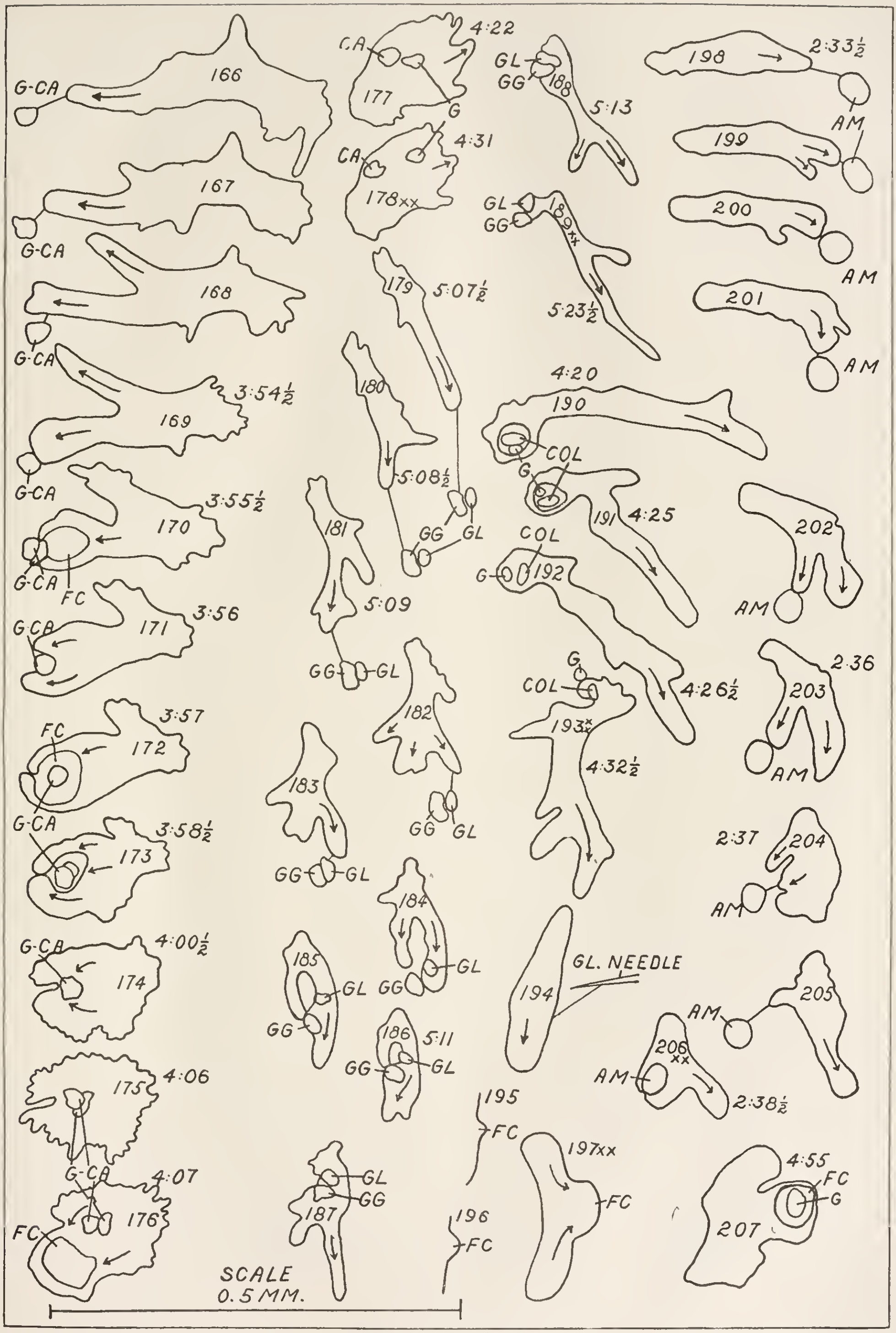
Figures 122—165.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4:55
FC
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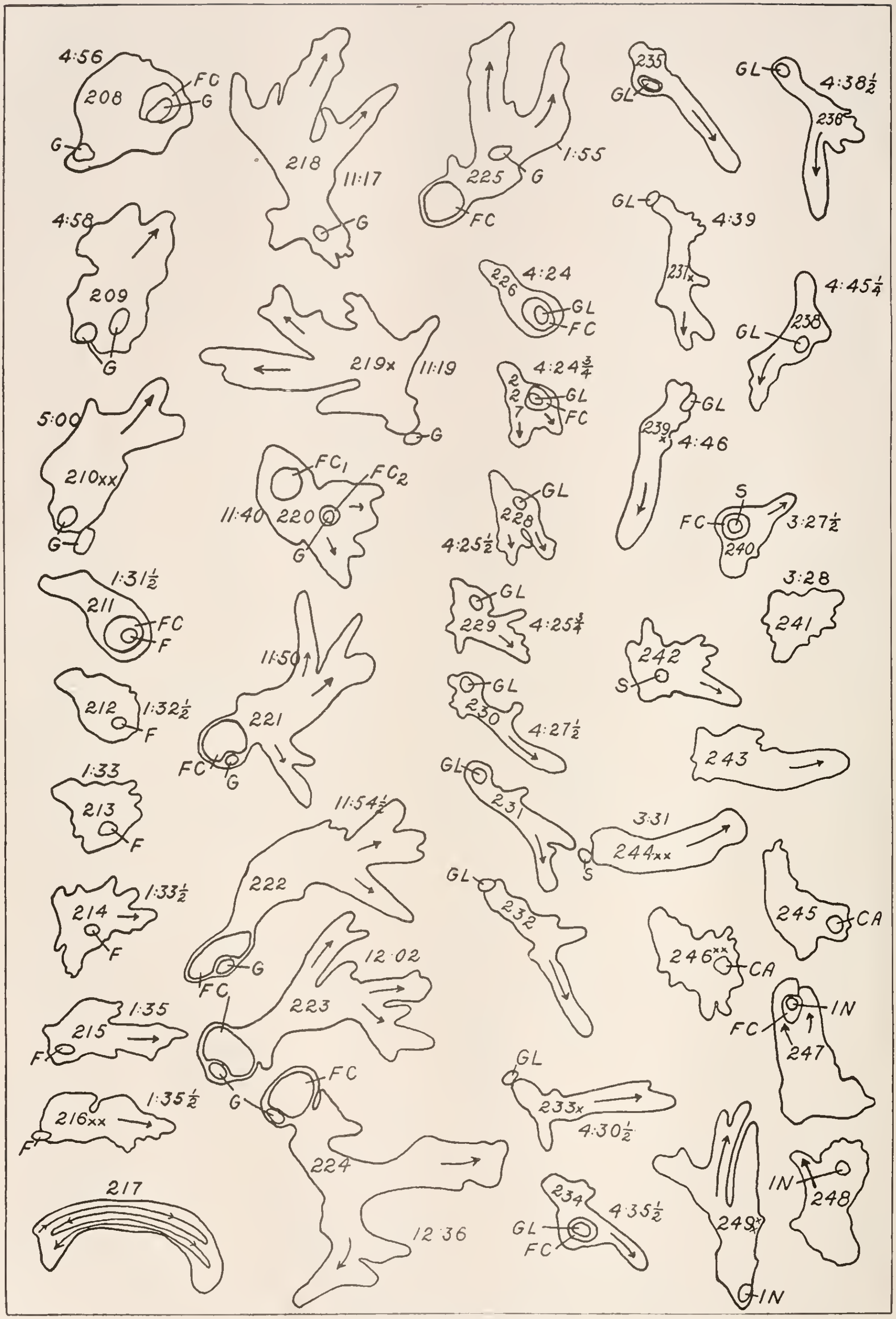
Figures 166—207.

PLATE 5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S
243
1:33
213
F
11:54½
GL
231
3:31
244xx
S
214
1:33½
F
222
G
FC
GL
232
245
CA
12:02
223
246xx
CA
1:35
215
F
IN
FC
247
G
FC
GL
233x
4:30½
1:35½
216xx
F
224
12:36
234
4:35½
GL
FC
IN
248
217
249x
IN

Figures 208—249.

MAZE STUDIES WITH THE WHITE RAT

I. Normal Animals

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INTRODUCTION

The work of Watson, Bogardus and Henke, Vincent, et. al. has shown that the white rat learns the standard type of maze primarily in tactual and kinaesthetic terms, that during the learning the control is gradually transferred from contact to kinaesthesis, and that after the problem is thoroughly mastered the act is to be regarded as a kinaesthetic-motor coordination with an occasional reliance upon contact in times of emergency.

The neglect of the senses of vision, audition, and smell in the process of acquisition is not due to any functional incapacity of these senses. Miss Vincent has demonstrated quite conclusively that with a proper arrangement of the mazes both vision and smell will be effectively utilized in the development of the maze habit. Neither can it be affirmed that no optical, auditory, or olfactory data are present in the standard maze situation; rather we must conclude that for the rat organization these data as compared with those of contact and kinaesthesis are inadequate for the solution of this particular kind of a problem. The maze habit can be regarded as a definite sensorimotor coordination which was developed and which functions within a larger sensory environment. Many of these environing sensory conditions remain relatively constant and stable during the mastery of the maze.

Our experiments were designed to test the dependence of the maze coordination upon the stability of the wider sensory environment in which it was developed. The method consists of varying these environmental conditions while the maze is being learned or after it is mastered. In the usual type of experiment the rats are transferred from the living cage (kept in a constant position) to the maze located in a different environment. It is thus possible to alter the sensory conditions of the animal while running the maze, or to effect changes in the environment prior to the test.

Various maze patterns were employed in the experiments. Unless otherwise stated, the mazes were of the usual type with the exception that they were almost water tight and covered by closely fitting glass covers. These features are mentioned because presumably they may effect the sensory relation of the animal to the extraneous environment. In order to alter the objective environment of the maze, recourse was had to a canvas top. A light but rigid frame was constructed and placed upon the maze. Over this was stretched several thicknesses of canvas fastened at the top but hanging loose on the four sides. From the top was suspended an electric lamp. The interior could thus be illumined or darkened, any of the four side curtains could be raised or lowered, or the whole top could be removed or replaced at will.

This paper describes the experimental results on animals with intact sense organs. Nearly two hundred rats were utilized in the various tests. Some of the results were secured by students working under my direction. The majority of the tests were performed by the writer.

The disturbances induced by the alterations were measured in terms of the error record. These records embrace such features as the number of animals affected, the number of trials in which error was present, the number of errors, the length of time necessary to adapt to the novel situation, and the tendency for the disturbing effect to be carried over to subsequent tests under normal conditions.

EXPERIMENTAL RESULTS

A. Alteration of conditions previous to running the maze.

Variable Route. In the typical experiment the living cage is kept on a rack some distance from the maze and the animals are carried by hand and placed within the maze. This route was kept constant while the maze was being mastered. After mastery this route was altered in various ways. Sometimes a long and devious route through the laboratory was chosen. Fourteen rats were tested and no disturbing effects were noted.

Method of Handling. The normal method of handling was varied by inducing a condition of dizziness just before placing the animals in the maze. The rats were held at arm's length and whirled rapidly around in horizontal and vertical circles and then placed in the maze. The dizziness effects were evident in the animal's behavior. They experienced difficulty in standing erect, crouched down on the floor of the maze, and waited for the effects to disappear before attempting to run. Twelve animals were employed and no disturbances were present.

Position of Cage. After the maze was learned, the living cage was transported to a new position in the laboratory, care being taken to preserve its original cardinal orientation. This alteration introduces two new features, a new route to the cage, and a new sensory environment previous to the maze reaction. Since variations in the route are without effect, this aspect of the alteration may be neglected. The duration of the exposure to the novel environment prior to the test was varied; the animals were tested either 15 minutes or 24 hours after the alteration. The distance over which the cage was moved also varied. Ten animals were tested. Seventy per cent of these were affected, and the disturbance was present in but 41 per cent of their trials. The degree of disturbance varied with the degree of alteration. One group of six rats was subjected to alternating small and large shifts in the position of the cage and the resulting average error records were .58 and 1.75 respectively. The animals quickly adapt themselves to these changes. Most of the disturbances resulted from the 15 minute exposures and in this case the disturbing effect had generally disappeared on the subsequent day's test. There was no evidence that the effects persisted for any length of time after a return to normal conditions.

Covering Cage. After the maze was mastered, the living cage was entirely covered with several thicknesses of canvas. This substituted a homogeneous for a heterogeneous visual environment and reduced the illumination of the cage very appreciably. The animals were kept in this environment for a day before the first test. Forty-five animals were subjected to the experiment. But one rat exhibited signs of disturbance and the effect was present only in the first day's test.

Rotation of Cage. The living cage was rotated in reference to the cardinal positions while remaining in the same position.

The shifts employed were 90, 180, 270 degrees. The duration of exposure to the novel conditions prior to the test was varied. Three groups of animals were utilized and the conditions differed so that a separate description for each group is necessary.

1. The first group consisted of six rats and both living cage and the maze were uncovered. The rats were first subjected to the new orientation for 15 minutes and then tested in the maze. The cage was then returned to its normal orientation and control tests were given on the second day. On the third day the animals were tested for the effects of a 15 minute exposure to a different orientation. No animal was disturbed by these 15 minute exposures. Exposures of 24 hours were given for three orientations on successive days. All of the rats were disturbed by these alterations. The average error record per trial for six tests was 2.86. Errors were present, however, in but 40 per cent of the trials. There was a marked individual difference in susceptibility, the number of errors ranging from 3 to 44. The degree of the disturbance increased with successive shifts, though the rats quickly adapted themselves when kept in a given orientation.

2. The cage was covered with the canvas top and then rotated. The animals were tested in an uncovered maze. The group consisted of forty-five rats. They were tested immediately after the rotation and then for several days in succession. Three successive shifts were made before the cage was returned to its normal orientation. But seven of the rats manifested signs of disturbance and the effect was slight and quickly eliminated. With one animal the effects were sufficiently obvious that a disturbance can hardly be doubted. The effect was present for the first day's test for two positions.

3. In this experiment the uncovered cage was rotated, and the animals were tested in a covered maze. The animals were subjected to one or more day's exposure to each new orientation before being tested. Seventeen animals were employed, and signs of disturbance were noted for but five. The effect was so slight in four cases that one cannot be confident of the results. The disturbing effect was obvious for one rat for two of the new positions.

B. Alteration of conditions while running the maze

Degree of Hunger. After the maze was mastered, periods of four days of heavy feeding were alternated with similar periods of normal feeding. We thus have the rats coming to the maze with different degrees of hunger, the object of the test being to determine the effect of strength of motive upon the accuracy of a well automatized act. Rats differ very materially in the length of the feeding period necessary to keep in good condition and to give consistent daily records. These individual differences are due to the rate of eating and the amount of food required. The normal time allowed for eating ranged from 5 to 7 minutes. The periods of heavy feeding were 15 to 20 minutes in length, the animals being allowed to gorge themselves to their utmost capacity. Ten rats were tested. Heavy feeding multiplied the average error record by twenty. All rats were affected in varying degrees. Disturbance was present in but one-third of the trials. The degree of the disturbance was highly irregular from trial to trial. In general the effect increased at first and then decreased. Complete adaptation was never secured.

Cleansing Maze. During the course of a long experiment, the maze will accumulate considerable filth in spite of the glass cover. This filth consists of faeces, wisps of cotton, shells of sunflower seeds, trackings of milk, and urine deposits. These were allowed to accumulate for considerable time and the maze was thoroughly cleansed and washed. The animals were tested on subsequent days to determine the effect of this alteration of conditions upon the accuracy of the maze habit. Ten rats were tested, and eight were affected. The greatest effect occurred on the second trial. Adaptation was secured in four trials. Errors were present in but 60 per cent of the tests. The average error record per trial for those affected was 1.75.

Covering Maze. The rats were allowed to master the uncovered maze. The canvas top described in the introductory section was then placed over the maze. In one case the interior of the top was illuminated when the rats were tested, and with another group it was not. A homogeneous maze environment was thus substituted for the customary heterogeneous one, and the illumination was either decreased or altered in character. Eighteen rats were subjected to these changes while running the maze, and none were disturbed in the slightest degree. This fact would indicate that the rat does not rely upon stimuli from the extraneous environment during the later stages of the learning process.

Uncovering Maze. The animals first mastered the maze while it was covered with the canvas top. After mastery this top was removed and the animals tested. Two slightly different experiments were performed. 1. The maze was mastered when the top was open on one side allowing poor daylight illumination of the interior. The top was now removed. Seven rats were tested and none were disturbed by the changes. 2. The maze was mastered while entirely closed and the interior illumined by an electric light. The top was now removed. There resulted the substitution of a heterogeneous for a uniform optical environment, and the introduction of daylight for artificial illumination. Ten rats were tested, and five were disturbed. The effects persisted from 1 to 6 trials. The errors were distributed irregularly, and perfect records were secured in 70 per cent of the tests. The average error record for those affected was 1.07 as compared with a previous normal of .20. The total number of errors per animal varied from 3 to 11.

Increase of Illumination. The maze was learned while entirely covered with the canvas top but without interior illumination. The interior was now illumined by the electric light. A well lighted uniform environment was thus substituted for a subdued one. Ten rats were tested, and seven were affected. The disturbance lasted from 1 to 6 trials. Errors were present in but 40 per cent of the tests. The average error record was 1.35 as compared with the previous record of .51. The total number of errors per individual varied from 4 to 47.

Decrease of Illumination. An open maze was mastered. It was situated in front of an open window giving a good illumination. After the maze was learned this window was covered so that practically all light from this source was excluded. This procedure decreased the illumination in the maze and altered its direction, without changing the character of the environing objects. Ten rats were tested and seven were disturbed. The effects lasted for 1 to 8 trials. The maximum effect occurred on the second test. Many trials were without error. The average error record was 3.18 as compared with a previous normal of .21. One animal made 40 errors in eight trials. After adaptation to the new conditions, a return to the normal situation effected no disturbance.

Position of the Experimenter. The experimenter maintained a constant position in reference to the maze while it was being learned. After mastery, this position was varied. After inserting the rats in the maze, the experimenter occupied a position on the opposite side of the maze from that in which he formerly had stood. Six rats were tested on successive days until all disturbance had subsided. All members of the group were affected in varying degree. Errors were present in 60 per cent of the tests. The average error record for three successive trials was 2.50 as compared with a previous normal of .11. The disturbance was eliminated in three trials. The total number of errors per rat for the three trials ranged from 2 to 18. The disturbance occurred only at that point in the maze path near which the experimenter stood. The path previous to and after this critical point was traversed normally. All error deviations were in the direction of the experimenter. A disturbance was frequently manifested by slow and hesitant movements and head and body orientations in the direction of the experimenter even when no errors were made.

Rotation of a Uniform Environment. The maze was covered by the canvas top closed on all sides and the interior was illuminated by the electric light. Under these conditions vision of the objective environment was impossible to the human eye. This top was practically square (3′, 9″ by 4′), and as a consequence the optical environment was uniform. The top was now rotated 90 degrees between trials, the maze itself remaining stationary. Presumably the visual situation was not altered by this procedure. Ten rats were tested, and no disturbance resulted.

Rotation of Heterogeneous Environment. The maze was learned with the curtain of the canvas top open on one side. This curtain was now closed and that on another side was opened. This procedure was continued until all four sides were opened several times on successive days. The alteration produced a change in the direction and intensity of the light as well as in the character of the optical environment. Seven rats were tested under these conditions, and five were affected by the novel conditions. These five animals made an average error record of 1.90 for six tests, and errors were present in 85 per cent of the trials. The disturbance due to the alteration persisted to some extent on the subsequent day's test in normal conditions. The number of errors per rat ranged from 9 to 15. A repetition of the test for each of the three novel situations exhibited a pronounced tendency toward adaptation, but the experiment was not continued until complete adaptation was secured.

Position of the Maze. After being learned, the maze was removed to a new position in the laboratory but its original cardinal orientation was preserved. The maze was shifted about twelve feet in position but the shift was of such a character that the maze was now situated in practically a new environment. This procedure involved two alterations; a change in the objective environment while running the maze, and a new route from the living cage to the maze. The latter factor has been shown to be non-effective and may thus be disregarded. Six rats were given three tests in the new position, and four were affected. These made errors in 55 per cent of the trials, and gave an average error record of 2.08. The number of errors per rat ranged from 4 to 10. The animals adapted quickly to the novel conditions, and in some cases a slight disturbance was evident on a return to the old position.

Rotation of Maze. In this experiment the canvas top was not used, and as a consequence the maze was rotated in reference to a stationary heterogeneous environment. This experiment was first performed by Professor Watson and our results are in harmony with those secured by him. Unless otherwise specified, the three novel positions utilized were 90, 180, and 270 degrees. The tests were conducted on different mazes and with different procedures and thus need to be described separately.

1. The glass covered maze was used and tests were given for the three novel positions on successive days followed by a return to the original position on the fourth day. This procedure was now repeated to determine the effect of adaptation. Ten rats were employed and all were disturbed. In the first shift, errors were present in 65 per cent of the trials, and an average error record of 6.95 was secured. The induced effect was occasionally carried over to the subsequent day's trial in the normal position. A repetition of the shifts disclosed a pronounced adaptive tendency. All members of the group were

still affected but the percentage of perfect trials was increased from 35 to 53 and the error record was reduced from 6.95 to 1.72. The shifts were not continued until complete adaptation was effected.

2. The same conditions obtained in this experiment except that the maze was left in each new position until the disturbance was eliminated. After adapting to the three positions, the maze was returned to the normal position. This procedure was now repeated until complete adaptation was effected for the four rotary positions. Similar rotary shifts were now instituted between the 45, 135, 225, and 315 degree positions until adaptation for these positions was effected. Fifteen animals were employed in the experiment. During the first rotation, thirteen animals were disturbed, and these gave an average error record of 10.7 for the first day for the three new situations. The rats were not affected in every trial, as perfect records were secured in 32 per cent of the first day's trials. Adaptation was effected for each position on an average of four trials. The induced disturbance was occasionally carried over to a slight extent to the normal position of the maze. The adaptation for each position secured in the first shift was not permanent. New rotations disclosed a further disturbance, but the effect gradually decreased with repeated shifts; fewer animals were disturbed, the errors became smaller, the percentage of perfect trials increased, there was less carrying over to the normal position, and the time necessary to adapt for each position was lessened. Complete adaptation was effected on the fifth repetition and thereafter the maze could be rotated at will between any of these four positions without disturbance. Complete adaptation for one series of positions does not, however, involve adaptation to another series of positions. Rotary shifts were now instituted between the 45, 135, 225, and 315 degree positions. In the first shift all of the rats were again disturbed. In the first day's trials for the four positions, the average error record was 7.2 with a percentage of perfect runs of 20. Adaptation was again effected with repeated tests.

3. A group of animals was rotated in a well illuminated and a darkened environment. The maze had been learned with the illuminated condition. The room was darkened by means of window shades. The animals were accustomed to running the

maze under both conditions before the rotation tests were given. One set of four rats were tested for three positions on successive days when the room was well illuminated. The tests were now repeated for the darkened environment and these were followed by a series with an illuminated maze. The average error records for the three conditions respectively were 7.15, 1.90, and 3.20. The final value for the illuminated environment is thus greater than that previously secured for the darkened condition in spite of the fact that animals tend to adapt to these rotary shifts when repeated. With a second set of six animals, complete adaptation was effected for three positions while the room was darkened. The room was then illuminated, and the tests were repeated. A disturbance was again evident. The disturbance could hardly be due to the sudden introduction of the light, as the maze had been learned under these conditions, and the rats had been accustomed to run the maze in its normal position while the room was illuminated. The results indicate that a maze rotation in reference to a well illuminated environment is more disturbing than a similar one in reference to a darkened environment.

4. A sideless maze was employed in the following experiment. This consists of a series of runways separated from each other by open spaces four inches in width. This maze differs from the standard maze usually employed in these experiments in several respects:—it is less complex as to number and length of alleys, the absence of sides eliminates the possibility of a contact guidance in traversing the paths, and the absence of the sides and the glass cover allows the animals a more intimate sensory contact with the objective environment. We were interested in comparing the degree of disturbance due to rotation on such a maze with that exhibited by animals in the standard maze. If rotation disturbs the animals because of the alteration in reference to the environment, the degree of disturbance in the sideless maze should be the greater. Five rats were tested. The average error record, and the number of trials necessary to secure adaptation were twice those for the standard maze. This ratio does not adequately represent, however, the relative confusion in the two cases because it neglects the greater simplicity of the sideless maze. If the two mazes offered equal opportunity for error, it is safe to assume that the discrepancy

between the two sets of values would have been much greater than they were. This difference in complexity can be equated by comparing the initial error record due to rotation with the initial error record in learning. The average error record for the first trial in learning the standard maze was 44, while the average number of errors made in the first rotation test was 10. Rotation in the standard maze produces an initial error disturbance which is approximately 23 per cent of that in mastering the maze. The initial error record for the sideless maze was 10.5, while the corresponding value for rotation was 19.7 The confusion involved in rotation was thus greater than that in learning. Relative to the number of initial errors in learning, rotation in the sideless maze produces a disturbance eight times as great as in the standard maze.

Certain peculiarities of behavior were apparent in the sideless maze. The rats frequently gravitated to that corner at which the food box had been located before the rotation. Failing to find food, they renewed their explorations of the maze, but came back again and again to this particular corner. One animal finally refused to leave this locality and had to be removed from the maze. After two such unsuccessful trials on successive days, the experimenter guided the animal to the new position of the food box, and thereafter the maze was traversed successfully on the animal's own initiative. One other rat was unsuccessful on the third trial. This type of behavior was exhibited in varying degrees during the first three trials by each of the ten rats employed in the test. Such behavior has been observed but rarely in a standard maze and only when certain parts of the maze were flooded by strong daylight illumination.

5. The *cul de sacs* in the standard maze were closed by sliding doors. After learning the maze in this condition, the animals were subjected to the usual rotation tests. Obviously all disturbance due to rotation must be measured by return errors. Twelve rats were tested and all were affected. The experiment is significant in indicating that the disturbance in maze rotation is not due exclusively to wrong choices at those critical positions from which several paths diverge. Confusion obtains when no choice is possible and when the animals have had no experience with *cul de sacs* during learning.

Rotation of Maze and Environment. The maze was learned while entirely covered by the canvas top and illuminated by an electric light. After learning, both maze and top were rotated as a unit. Tests were given for the three positions on successive days. On the fourth day a normal record was secured for the original position. The above procedure was then repeated several times. Ten rats were utilized in the experiment. In the first shift eight rats were disturbed; these gave an average error record of 1.29 for 48 trials, although errors were present in but 31 per cent of the trials. The shifts were now repeated three times and no tendency toward adaptation was in evidence. The percentages of animals affected in the four successive shifts were 80, 80, 90 and 70. The percentages of trials in which error was present were 31, 35, 55, and 36. The error records were 1.29, 1.81, 1.18, and 1.32. The largest disturbance occurred for the 180 degree position. This result is a function of the position and not of the temporal order of the shifts, inasmuch as a different temporal order of the three positions was given in the successive series.

This experiment is comparable with the first test of the previous section in all respects except the environmental conditions. In the previous test the maze was rotated in reference to the environment, while here both maze and environment were rotated. Rotation in reference to a stationary environment produced much the greater effect at first, and allowed a pronounced degree of adaptation when the experiment was repeated. No adaptation was present when both maze and environment were rotated, and the records secured were practically identical with those in the former experiment after the rats had become adapted.

C. Alteration of conditions while learning the maze

Rotation of Maze. Animals were required to master the standard maze when its cardinal orientation was changed for each day's test. The daily shifts in position were 90 degrees, each position being repeated every fourth day. These records are compared with those representing the mastery of a stationary maze, and we are able to estimate the relative effect upon learning of a stable vs. a variable relation to the objective environment. The following records for a rotated maze were obtained from ten rats without previous laboratory experience:—the average number of trials involved in mastering the maze was 30, a group error record of zero was first obtained on the 36th trial, and the average number of errors made during learning was 196. The corresponding values for a group of 29 rats learning the same maze while stationary were 18, 22, and 144 respectively. Rotation thus increased these values by 50 per cent. A comparison is likewise possible between two groups of rats which had had previous experience upon a different type of problem. Ten rats in learning a rotated maze mastered it in 21.4 trials, first secured a perfect group record on the 27th trial and averaged 110 errors per rat for the learning period. The corresponding values for 14 rats in mastering the same maze while stationary were 9.2, 17, and 58. In this case rotation has doubled the difficulty of learning. The two curves of learning were similar in form; rotation seems to add on the average about 3 or 4 errors to each trial and this slight addition towards the end operates to postpone the final mastery of the maze for many trials.

Uniform Environment. Certain groups of rats mastered the maze when covered on all sides by the canvas top. Other groups also mastered this maze without the top. In one case the maze habit was developed in a uniform optical environment, and in the other with a heterogeneous environment. A comparison of the two sets of data will thus indicate the function of a heterogeneous environment in the development of a habit. The heterogeneous environment aided learning. The average number of trials and the average number of errors per rat for a group of 29 rats in mastering an open maze were 18 and 144 respectively. The corresponding values for the closed maze were 26 and 282. These results indicate that the animals may utilize data from the objective environment in mastering the maze.

CONCLUSIONS

Any sensori-motor act can not be regarded as an isolated independent function; the act was learned within a wider sensory environment, and it never ceases to be wholly free from these conditions either during or after its development. The stability of the environment furthers the development of the act, and conditions the regularity and accuracy of its functioning after it has become automatic. These environmental conditions embrace the sensory situation at the time, the sensory situation in which the animal lived for several days prior to the act, as well as the intraorganic condition of the animal. The influence of intraorganic factors is evident from four types of facts:—1. The case of hunger is obvious. 2. Novel situations while running the maze may induce effects which persist and exert a disturbing influence after a return to normal conditions. These persistent disturbing effects must be intraorganic. 3. Alterations of the cage environment previous to the performance of the act may exert a disturbing effect. Evidently these disturbing conditions must be retained as some intraorganic condition. 4. The influence of some of these alterations may be cumulative from day to day.

These alterations operate in an irregular and sporadic fashion. This generalization is supported by several lines of evidence. 1. A few animals in each group are usually immune to the altered conditions. In the majority of experiments the percentage of animals affected ranged from 50 to 90. 2. Animals may be disturbed in one trial but immune in another. The percentage of trials in which error was present ranges from 30 to 65 for the various experiments. On the average the affected animals were not susceptible to the alterations in one-half the tests. 3. An animal may be susceptible to one kind of alteration but immune to another, while the opposite relation will obtain for another rat. Eleven rats were subjected to the following five experiments,—position of experimenter, rotation of cage, position of cage, position of maze, and rotation of maze. Three animals were disturbed in all five experiments, three rats were affected in but four tests, two rats in three tests, two rats in two experiments, and one rat in but a single test. Two rats were disturbed by the rotation of the maze, but were not affected by a change in the position of the maze; on the other hand, two rats were disturbed by the latter test but were immune to the rotation of the maze. Ten rats were given the following tests, increase of illumination, rotation of maze and environment, cleansing paths, uncovering maze, and rotation of maze. One rat was affected by all tests, three rats were immune to one experiment, four to two experiments, and two to three experiments. Three animals were immune to the rotation of the maze and environment, but were disturbed by cleansing the maze; on the other hand two rats were immune to the changes involved in the cleansing of the maze but susceptible to the first experiment. Many similar illustrations can be given. 4. A rat may make a very large number of errors in some tests and very few errors in others. Ten rats were ranked as to the number of errors made in each of five experiments. The rankings given to one rat for the five experiments were 1, 2, 9, 2, and 2. Similar rankings for another animal were 8, 1, 1, 7, and 9. This lack of consistency may be shown by dividing the animals into two groups on the basis of number of errors. Only one of the ten rats belonged to the better half in all five experiments. In another group of eleven rats but four manifested any high degree of consistency; two were found in the better half for all experiments, while two invariably belonged to the poorer half. The rankings for one experiment were correlated with those for the other four experiments, and positive values of .369, .690, .414, and .068 were obtained. 5. Affected animals make a relatively high percentage of perfect runs in one experiment and a low percentage in another. 6. One would naturally expect a high degree of correlation between the total number of errors made in an experiment and the number of trials in which a disturbance was present. Two groups of animals were ranked in both respects for five experiments and the correlation values were computed. Small negative values were obtained in every case. These results mean that those animals which make an extremely large number of errors in one trial are likely to become adapted to the alteration and run the subsequent trials without error. 7. Animals that do well for one position in the experiment on maze rotation do not necessarily make good records for other positions. The correlation value between two positions for a group of nine rats was but .434. Animals that do well for one position do not necessarily make good records when the test for this position is repeated. Such a correlation by the ranking method for the above group of rats gave a value of but .024.

The above emphasis upon the irregular and accidental character of the disturbances must not blind one to the fact that some rats manifest a relatively high degree of consistency in the various experiments. Some animals are quite susceptible and make a large number of errors in every experiment. Other rats are prone to immunity; they either fail to be disturbed or make low error scores in every experiment. This consistency is limited to comparatively few animals; irregularity and inconsistency obtain for the majority of the rats and for the groups taken as a whole.

Adaptability to these alterations is the general rule. The rate of adaptability is a function in general of the magnitude of the disturbance. Stability of the novel conditions aids adaptation, while any further change delays it; animals kept in a novel situation eliminate the disturbance more quickly than when they are shifted back and forth between the novel and the normal conditions. Continuous alterations of the novel conditions as in the various rotation experiments operate to delay the adaptation. Adaptation to any novel situation is in the main specific and not general; the animals become adapted to that particular alteration and not to all novel situations. There is no conclusive evidence that the adaptation secured in one experiment operates to give complete immunity in other experiments. Complete adaptation to one series of positions in the rotation experiment did not involve a complete immunity for alterations between another series of positions. Any adaptation to a particular situation is retained with some degree of perfection over a period of time devoted to securing adjustments to other novel conditions. Any acquired immunity is thus mainly specific and refers only to that situation under which it was acquired; it is retained after the interpolation of other tests with some degree of perfection, but it gives no certain aid to the mastery of other novel situations.

The degree of disturbance was a function of the kind of alteration. As a general rule alterations while running the maze were more effective than changed conditions of the rat's environment before being placed in the maze. It is rather surprising that pronounced changes in method of handling and of route from cage to maze should be without effect, while alterations of the living cage in relation to its environment were provocative of error. The difference in the results may be due to the fact that the animals were not subjected to a sufficient duration of exposure to the novel conditions in the former two experiments. The maximum duration of exposure never exceeded a few minutes, while the minimum exposure in the cage experiments was fifteen minutes. Covering the maze produced no effect, while considerable disturbance was manifest when the maze was uncovered. This difference in results is more comprehensible when the situation is stated in the following terms:—The removal of stimuli (change from a heterogeneous to a uniform environment) is without effect, while the introduction of novel stimuli operates as a disturbance. This conception would indicate that the rats after mastering the maze do not rely to any great extent upon the objective stimuli as guides or controls in traversing the maze, and that the introduction of unfamiliar conditions operates as a distraction.

This paper makes no pretense of defining in physical terms the nature of the environmental alterations. Rotation of the maze may disturb the normal relation of the animal to the optical, olfactory, or auditory aspects of the environment. Likewise we make no pretense of knowing through what sense avenue these disturbances were mediated. We were interested primarily in establishing the fact that the rats are sensitive to these alterations in some way and that stability of sensory conditions is conducive to the development of an automatic act.

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MAZE STUDIES WITH THE WHITE RAT

II. Blind Animals

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In the previous paper there was formulated the proposition that the maze habit is dependent to some degree upon the stability of various environmental conditions. The present paper concerns the function vision in sensing these alterations and becoming adapted to them. The method consists of comparing the records of blind rats with those of animals with intact sense organs. The possibility of vision was eliminated by the usual method of extirpation of the bulb. Three of the rats were subjected to an autopsy and a microscopical examination by Professor C. J. Herrick, who reports that all three were probably blind. Comparisons will be facilitated by certain classifications of the experiments.

1. The first group contains all those experiments in which no blind animals were tested, and hence comparisons are impossible. This group consists of the following experiments. Covering cage, covering maze, increase of illumination, decrease of illumination, rotation of a uniform environment, the second phase of uncovering the maze, and the 3rd, 4th, and 5th tests on rotating the maze.

2. The second group contains those experiments in which both seeing and blind animals were utilized but in which no rats were disturbed by the alterations. Obviously these experiments can furnish no data as to the function of vision. Nine blinds

were subjected to the "variable route" test and none were affected. Five blinds were tested on variations of method of handling without disturbing results. Two blinds were subjected to the first test on uncovering the maze and no effect was noticeable.

3. In the third class fall those experiments in which both blind and seeing rats were tested, but in which the disturbance was limited to those animals with vision.

Alterations in the position of the experimenter affected none of the five blind animals tested, while every member of a group of six normal rats was disturbed.

A change in the position of the maze had no effect upon any member of a group of five blind animals. In a group of six normal rats, four were affected and these made an average error record of 2.08.

4. In the remaining experiments, both blind and normal animals were tested and both groups were disturbed. The comparative records will need to be stated in detail for each experiment.

Degree of Hunger. Two blind rats were compared with ten normals. All members of both groups were disturbed. The blinds made errors the more frequently; the percentages of trials with error being 42 and 34 respectively for the blind and visual groups. The average error records for the two groups were 9.75 and 2.38 for the blinds and normals respectively. The blinds manifested their maximum of disturbance on the third trial while the normals gave the largest error record on the fifth trial. The blinds also exhibited the greater error record on a return to normal conditions.

Cleansing Maze. Seven blinds were compared with ten normals. Fewer blinds were affected, the percentages being 57 and 80. They made errors in 75% of their trials as compared with 61% for the normals. Their average error record was 6.00 as compared with 1.70 for the normals. Their greatest disturbance occurred on the first trial while the normals made their poorest record on the second trial. The time necessary to effect an adaptation was the same for the two groups. The blind animals exhibited the greater range of variability as to number of errors per rat; the average and the average variation for the blinds were 24.0 and 18.6 respectively, while the corresponding values for the normals were 10 and 5.6. The average variation relative to the size of the errors is thus much greater for the blind group.

Position of Cage.—Both groups contained ten rats. A smaller percentage of the blinds was affected, the values being 40 and 70. Those blinds affected were disturbed in a greater percentage of their trials (50 vs. 41), and made the greater average error score (1.33 vs. .87). The blind animals require a longer duration of exposure to induce an effect; they were disturbed only for the 24-hr. exposures, while the normals were affected by a 15-min. exposure. The blind rats also possessed the poorer adaptive power, for the normals became so accustomed to the novel situation in 24 hours that a disturbance was no longer manifest.

Rotation of Maze. Two blinds were tested on the first type of maze rotation, in which the three positions were tested on successive days. Their records are to be compared with those of ten normals. All members of both groups were disturbed. The blinds made errors in a greater percentage of their trials (67 vs. 65), but their average error record was much smaller (3.33 vs. 6.95). With a repetition of the test the poorer adaptive ability was manifested by the animals without vision; they decreased the percentage of trials in which error was present from 67 to 58, and their error record from 3.33 to 2.50. The visual group on the contrary reduced their error record from 6.95 to 1.72 and the percentage of runs with error from 65 to 47.

Rotation of Heterogeneous Maze Environment. The records of fourteen blind animals are to be compared with those of seven normal rats. A greater percentage of blind rats was disturbed (78 vs. 71). The errors of the blind group were confined to a smaller percentage of the trials (38 vs. 83). The blinds gave the larger error score (2.32 vs. 1.90) in spite of the fact that the errors were limited to fewer trials. The discrepancy is much greater when we compare the total number of errors per rat (18 vs. 12). The blinds exhibited the greater range of variability as to number of errors per rat; for the blinds the errors ranged from 3 to 70 with a mean variation of 15. The range for the normals was 9 to 15 with a mean variation of 2.2. The normal rats appeared to react definitely to the altered conditions. With each new change of conditions the errors were made at those places in the maze where the lighting conditions were altered the most. The blind animals, on the contrary, gave no evidence of reacting specifically to any observable changes. The errors were likely to occur anywhere within the maze. When the experiment was first performed, a group of four blinds was employed mainly as a control as no disturbance was expected. Since the number of errors was increased beyond the normal records, the test was repeated upon two other groups of blinds consisting of five each. The same results were obtained; the rats did not seem to be reacting to any specific feature in the environment and yet the normal number of errors was increased; some rats occasionally became almost hopelessly confused. Five animals made over 17 errors in a single trial.

Rotation of Maze and Environment. The records of five blinds are to be compared with those of ten normals. Eighty per cent of each group was disturbed. The blind animals made errors the more frequently, the percentage of runs with error being 42 and 31. The average error records of the blinds and normals were 7.76 and 1.29 respectively. The blinds exhibited the greater range of individual variability; the individual number of errors ranged between 3 and 172 for the blind rats and between 2 and 22 for the normals. The test was not repeated for the blinds so that comparisons as to adaptability are impossible. The blind rats, however, exhibited more disturbance after a return to normal conditions.

Rotation of Cage. Nine blind rats were tested. For the 15-min. exposure, all were affected, errors were present in 57% of the trials, and the average error record was 1.90. For the 24-hr. exposure, 90% were disturbed, errors were present in 62% of the trials, and the average error record was 4.95. A repetition of the tests disclosed no tendency toward adaptation.

Blind rats are more susceptible to these alterations than are the normals; blinds were disturbed by the 15-min. exposure while the normals were not. The blinds were also affected more by the 24-hr. shifts than were animals with vision. The blinds exhibited the greater range of individual variability as to number of errors, and the lesser powers of adaptability.

5. We are also able to compare the records of blind and normal animals in the mastery of the maze problem.

Vision aids untrained rats in learning a stationary maze, decreasing the number of trials by 28% and the total number of errors by 27%. The following records were obtained for 19 blind animals. The average number of trials involved in learning was 25. A perfect record was secured for the various groups on the 30th trial. An average total of 229 errors was made by each rat. The corresponding values for 27 normal animals were 18, 22, and 144. The generalization that vision may aid in the mastery of a stationary maze contradicts the findings of Watson in his study of kinaesthetic sensitivity. I do not question these results but doubt their universality. In these experiments the records of many blind rats and the average records of many groups of blind animals do not suffer in a comparison with the records of normal animals. One of the blind rats mastered the maze more quickly than any of the 27 normals. Two of the blind groups gave as good records as those of three groups of normals. On the other hand, six of the nineteen blinds did worse than the poorest of the 27 normals, and two groups of blinds gave a higher average record than the poorest group among the normals. While some individuals and some groups of blind animals do as well or better than the average run of the normal animals, yet there are many blind rats that do considerably worse than the majority of the normals. When the groups compared are rather large, there is likely to be a number of blind rats with extremely poor records and these cases are responsible for the poor group average. The blind rats exhibit the greater range of individual variability in their capacity to learn.

Vision aids trained rats to learn the rotated maze, decreasing the values by 35-40%. A group of 10 normals learned the rotated maze in 21.5 trials with an average total error score of 110. The corresponding values for three blind animals were 33.3 and 190. The rats had previously been trained on an alternation problem. The size of the blind group is too small, however, for a confident conclusion.

Vision is a detriment with untrained rats in mastering a rotated maze, increasing both number of trials and total errors. A group of six blinds learned the maze in 27 trials with an average error score of 117. The corresponding values for 10 normal rats were 30 and 196.

6. There are certain other peculiarities of blind rats con-

nected with their greater variability and erraticness. Blind rats are rather difficult to keep in good physical condition. They are more inclined to sluggishness in behavior, their appetite is frequently diminished, their hair becomes dry and rough, and they are sometimes rather flabby and cold to the touch. I have also noted what may be termed as a "breakdown," of which a number of examples may be cited. A group of six normals had been employed for four months in a sound discrimination experiment. Their conduct was normal and their physical condition was excellent at the conclusion of the experiment. These animals were now blinded and given the maze problem. Four of these rats proceeded to learn the maze in a normal manner for a number of trials and then suffered the "breakdown." They made complete failures of their attempts, became exhausted before success was achieved, and finally refused to run when placed in the maze. The break came on suddenly and occurred between the 6th and the 15th trials,—after the maze had been pretty well mastered. In another group of four animals without previous experience, one rat made rapid progress up to the 12th trial and then refused to run. The breakdown may occur at almost any stage of the experimentation. I had one individual that refused to run in the first trial. Another rat broke down on the 142nd trial during the control tests,—long after the maze had been mastered. Sometimes the rats simply quit and refuse to work further. Others work industriously but fail to find the food box, and are finally forced to cease their efforts through exhaustion; this behavior may be repeated in a number of successive trials until the rat quits and refuses to work when placed in the maze. Recovery from these breakdowns is rare and the rats may as well be eliminated from the experiment. I have tested such rats for a number of days in succession, and once a week for a couple of months in the hope that an interval of rest would induce recovery. These animals may continue to live and enjoy the average of health for blind rats. Some have been kept in the laboratory for five to six months. I have had some females bear and rear young subsequent to the breakdown. The phenomenon needs extended and systematic study.

The above differences in the comparative data obviously must be explained and interpreted in terms of vision. Certain conclusions can be asserted with confidence. Some interpretations must be regarded as suggestive.

Vision has a sensitive function. This statement means that the various objective alterations sometimes affected the animal's behavior through the medium of vision; in ordinary language we would say that the changes were perceived through the eye. The sensitivity of the eye is sufficiently proven by the third class of experiments in which the disturbances were limited to those animals with vision. Obviously these alterations were sensed wholly through the eye.

Most of these alterations may be sensed entirely through some other sense avenue than vision. The novel sensory conditions in the hunger experiment were obviously intraorganic in character. Vision can hardly be concerned in a sensitive way. In most of the experiments, the blind animals were affected; these blind animals must have sensed the novel conditions by means of other sense avenues than vision.

The normal animals probably utilized both of the above sensory means in reacting to the novel features in the fourth class of experiments. They possess both sensory capacities. The alteration can be perceived through this other sense modality since the blinds were affected. The alterations certainly possessed optical features. The differential sensitivity of blind and normal rats indicates that these changes were sensed wholly or in part through vision. The normal rats exhibited the greater degree of susceptibility or sensitivity to the alterations. The percentage of animals affected among the normals was equal to or greater than that for the blind rats with the exception of one experiment,—rotation of the cage. Obviously, this exception can not be explained on the hypothesis that the blind rats possessed modes of sensitivity not belonging to normal animals: it can be explained, however, in terms of principles to be developed later.

Vision possesses a corrective and adaptive function. The presence of eyes in some way increases the ability of the animal to adapt to these changes. Normal animals resist and overcome the disturbances better than do the blinds. The effect of this function is found in the greater rapidity of adaptation, a smaller error record, and a larger percentage of perfect runs. The best illustration of the operation of this function is found in the hunger experiment. Both groups of animals reacted to these alterations through a common mode of sensitivity and the percentage affected was the same for both groups. Vision, however, operated to minimize and overcome the effects of the disturbing conditions. The normal animals were able to make more perfect runs; they were able to resist the distracting influences more frequently than the blind rats. When disturbances did occur, the normal animals made by far the fewer errors; vision decreased the number of errors. Animals with vision exhibited the greater tendency to adapt themselves to these novel situations; they also recuperated from the effects more quickly after a return to normal conditions. Comparing the records of the two groups in the various experiments of the fourth class, we find that the adaptive and recuperative power of the normals is equal to or greater than that of the blind animals in every case. The normal animals made a greater percentage of perfect runs with the exception of one experiment; evidently they are more able to resist the distractive conditions. Rats with vision gave the smaller error score in every experiment but one; they thus possess the power of minimizing the disturbance when it occurs. When comparisons are possible as to the correlation between the maximum disturbance and the duration of exposure to the novel conditions, we find that the normal animals are the more resistant in three of four cases. The blind rats invariably exhibit the greater variability as to the range of errors. Blind rats are extremely variable as to number of errors; they are more likely to go to pieces, become lost and run high error scores when they are disturbed; this fact would indicate that vision operates as a corrective and control.

The discrepancies and exceptions in the application of the above two principles of explanation become explicable when we consider that the two functions of sensitivity and adaptation are antagonistic in their effects. The greater the sensitivity the larger will be the number of animals affected, the percentage of runs with error, and the total number of errors. The corrective function will operate to decrease the number of errors and the percentage of runs with error; it might also decrease the number of animals susceptible to the disturbing changes. The two functions, although antagonistic in their effects, are not necessarily mutually exclusive; both may conceivably operate at the same time. The actual records secured in any experiment will thus be a function of the relative strength of the two tendencies. In one type of situation the sensitive function may be the more effective in determining the character of the records, while the adaptive function may be the more efficacious in another experimental situation. The two experiments which deviated from the usual rule were rotation of maze and rotation of cage. The average error score of the normals was less than that of the blinds with the exception of the maze rotation experiment. We have here a rotation in reference to a predominantly optical situation, and one would expect that the sensitive function of the eye would predominate in effectiveness; the disturbance is so great that the corrective effects are not sufficient to reduce the error record below that of the blind animals. When the test was repeated, we find that the normal groups made the greater adaptive progress, and reduced their error score below that of the blinds. When the corrective function is given time to become efficacious, the error records no longer constitute an exception to the rule. When the cage was rotated, normal animals were not affected by a 15-min. exposure, while the blind rats were. We may explain this difference in susceptibility on the hypothesis that the corrective function of vision enabled the normal animals to resist the disturbing effects of the new conditions. With a 24-hr. exposure both groups were affected, but the blinds manifested the greater disturbance and the normals exhibited the greater tendency toward adaptation. The normal rats thus were no longer able to resist the cumulative effects of a prolonged exposure, but the corrective function of vision enabled them to reduce the degree of the disturbance and hasten adaptation.

The corrective and sensitive functions of vision are also evident from a comparison of the records of normal rats in the different experiments. When the maze was rotated in reference to a stationary heterogeneous environment, the normal animals were exceedingly disturbed but they made marked progress in adaptation when the test was repeated. A rotation of the maze and a uniform optical environment gave a lesser degree of disturbance and no tendency toward adaptation. The difference in the two alterations was presumably optical in the main. The greater the optical changes, the greater was the sensitivity and the adaptive power of the animals. Likewise, when normal rats were rotated in an open and a covered cage, the greater sensitivity was manifested in the former case. Many similar illustrations can be given.

The terms "sensitive" and "corrective" have so far been used in a purely descriptive sense, to state certain differences of fact. As explanatory concepts they render but little service.

In attempting to explain the greater sensitivity of the normal rats to all alterations instituted after the mastery of the maze, two possibilities exist; these functions of vision we may term "directive" and "distractive." The first hypothesis assumes that the motor activity of the animal is guided and directed in part by the visual impulses released by the stimuli from the objective environment. When the relation between the rat and these features of the environment is altered, motor disturbances are the inevitable result. It is possible that this directive function of vision may be present during the mastery of the maze but absent after the act has been thoroughly developed. The distractive hypothesis assumes that the maze habit is influenced in no way by the visual environment so long as it remains stable. Any pronounced alteration, however, is sensed immediately and operates as a distractive stimulus; in common parlance, it attracts the animal's attention, the rat reacts to the new conditions, and as a consequence the maze habit is disrupted. These two functions are not necessarily mutually exclusive; it is possible that both may be efficacious in mediating the disturbance in any run through the maze.

Between the two explanatory conceptions, we are forced to conclude in favor of the distraction hypothesis as far as the normal animals are concerned. When the position of the experimenter was altered, the rats were never disturbed in that section of the maze near which the experimenter had been standing. In fact the animals were not disturbed at any position in the maze at which they were oriented towards the old position of the experimenter. This fact would indicate that the rats did not employ visual stimuli from this source in any effective fashion in directing and orienting their conduct in the maze. The disturbance did occur, however, in those sections of the maze near the new position of the experimenter and when the rats were oriented in his direction. When the animals left the true pathway, they invariably ran towards the experimenter. This positive reaction can not be considered a directive habit acquired in learning the maze because the conformation of the maze at the old position was such as to prevent it. The positive reaction can better be regarded as a feeding habit developed in the living cage and on the feeding table. The experimenter thus attracted the animal's attention because of the novelty of the position and stimulated an old habit acquired while the rat was being handled and fed. The arousal of this habit naturally disrupted the normal functioning of the maze act. In several experiments such as increasing and decreasing the illumination, rotating the maze in darkened and lighted environments, and rotating a heterogeneous environment, the following behavior was frequently noted: Animals suffered a pronounced disturbance at those points where the illumination had been greatly increased. I have frequently seen animals run the maze without error up to a point where an alley, customarily darkened, was flooded with a beam of strong daylight. Here the rat stopped suddenly, exhibited strong signs of nervousness and timidity with frequent retracing in search of another path. Decreasing the illumination in any part of the maze seemed to be without effect, but a pronounced increase was effective. These facts indicate that the alterations served as distractions. The distractive theory is further supported by the irregular and occasional character of the disturbances. This feature of the results was summarized in the first paper. It refers to such facts that many trials are without error, that rats are immune in one experiment and susceptible in another, and that the number of errors made in various trials is extremely variable. If the rats are relying upon the objective data to guide their conduct in the maze, it would seem that any rat should be disturbed in every trial until complete adaptation is secured. The fact that the disturbances occur in a perfectly haphazard and accidental manner is readily interpreted on the basis of the distractive theory. The disturbance is present only when the alterations attract the attention of the rat, and this result is largely a matter of chance. Conclusive proof of the distractive function is obtained from the comparative records on covering and uncovering the maze. Rats learned the uncovered maze,—a maze with a well lighted and heterogeneous optical environment. The maze is now covered with the canvas top. A uniform but darkened environment is substituted for that present while the maze was mastered. If the rat is relying upon these visual objects as directive stimuli in threading the maze, their sudden removal should disrupt the act. No animals were disturbed in this test, and we are forced to conclude that vision possessed no directive function after the maze was mastered. We may also assume that the alteration did not operate as a distraction because the new environment was homogeneous and poorly lighted. In the opposite experiment of uncovering the maze, we may conclude that vision of the extraneous environment possessed no directive function because the conditions were such that no possibilities were present for its development. The maze was mastered in a homogeneous optical environment. Removal of the top and the introduction of a well illumined and heterogeneous environment resulted in disturbances. Evidently these novel conditions were effective only as distractions. If we could generalize from these experiments, we would be forced to conclude that all disturbances due to alterations after the maze is learned and while the rat is running are the result of distractions.

There is but one possible exception to the above formulation,—certain characteristics of behavior when the sideless maze was rotated. After rotation the animals frequently drifted to that corner at which the food box had formerly been located. This fact would indicate that the rats can orient themselves in reference to the position of the food box in terms of stimuli emanating from the extraneous environment. The same behavior was occasionally noted in the rotation of the standard maze when the extraneous environment near the food box possessed unusual features, as an open window giving good light. Granted that this fact indicates a directive function, yet it is by no means certain that it was mediated through vision rather than smell or some other sense, for no blind animals were employed as controls in this experiment. The fact can be interpreted, however, in terms of the distractive function. It is possible that certain unusual features in the environment near the position of the food box operated as a distractive stimulus and that the rats reacted to it in a positive manner. We may then safely conclude that alterations instituted after the maze is mastered and while it is being run may and do operate as distractive stimuli in so far as they are sensed through vision; it is also possible that certain alterations may disturb the animal because these stimuli had been utilized as guides in running the maze, but no affirmative statements can be made with confidence.

Blind animals were also disturbed and this disturbance was mediated through other senses than vision; we must also assume that normal animals were disturbed in part through other modalities of sense than vision. This disturbance may also be explained by the assumption that these other senses were susceptible to the altered conditions either as distractions or as motor controls. There are no facts which support the directive hypothesis in a conclusive fashion. Certain facts can hardly be interpreted in other than distractive terms. The effect of varying the degree of hunger is obvious. The haphazard and occasional character of the disturbance was more characteristic of the behavior of the blind than of the normal animals, and this fact is best explained by the distractive hypothesis. The differential sensitivity of the normal and blind rats is thus one of degree and not of kind. Normal animals manifest the greater degree of susceptibility to the changes because they are affected through more sensory avenues.

The comparative learning records of the various groups of animals furnish certain data relative to the function of vision.

1. Normal rats master a stationary maze more readily than a rotated maze, and an open maze quicker than a covered one. These facts can be explained in terms of either the distractive or directive hypotheses. If the animal can utilize objective stimuli as guides or controls, the presence and stability of an optical environment should facilitate the learning process. Likewise these objective stimuli may function merely to attract the animal's attention, encourage unnecessary and disadvantageous excursions, and otherwise distract the animal from the more serious business at hand. On this hypothesis a changing environment would operate as a more effective distractor than a stationary one. Likewise, the distractive effect of a heterogeneous environment would be greater than that of a uniform one.

2. Rats with vision learn a stationary maze more easily than do blind animals. This poorer learning capacity of blind rats may be explained in numerous ways: a. We may assume that

the normal animals learn to utilize visual stimuli as controls in selecting the true path from the numerous *cul de sacs.* b. Vision may be advantageous because of the tonic effect of light. Visual stimuli exert a tonic and stimulative effect upon the various activities of the organism. Rats with vision exhibit the greater vigor and superabundance of bodily activity. Surplus activity is necessarily valuable in any trial and error mode of learning. This effect of light will also be manifested by the vital activities. Heightened vitality will be influential via of an increased retentive capacity or a stronger hunger motive. Decreased activity and vitality resulting from loss of vision may interact upon each other; decreased activity, or lack of exercise, will lower the vital tonus of the organism, and this lowered vitality will in turn produce sluggishness of behavior. c. We may assume that the learning capacity of blind rats has been minimized by certain deleterious effects of the operation per se. The connection between these effects and learning capacity may be conceived in several ways. The operation (the surgical shock or the effect of the ether) may act directly upon the vital activities and thus influence learning capacity as sketched above. The organic aftereffects may be conceived as some sort of a nervous irritant which operates as a distractive stimulus and thus produces erratic and exaggerated behavior. Likewise the effects may be nervous modifications of such a character as to render the animal more susceptible than usual to any novel stimulative conditions. The animal is thus prone to erratic, irregular and exaggerated modes of response detrimental to the mastery of the maze. On this hypothesis, stability and instability will characterize normal and blind rats respectively.

The last two hypotheses are supported by several lines of evidence. Blind rats frequently exhibit signs of decreased vitality such as muscular flabbiness, rough coats, poor circulation, poor appetite, and a susceptibility to disease. Blind animals are also less active as a general rule; the normal vigor, persistence, and superabundance of activity is frequently lacking. The phenomenon of breakdowns characteristic of blind rats also suggests the validity of the third conception. The greater erraticness and variability of blind animals,—the tendency to make now and then unusually large error scores, is explicable in terms of the third conception. There are no facts which directly support the first conception of a directive function of vision.

3. Vision is a detriment to the mastery of the rotated maze when untrained animals are utilized. This fact cannot be explained on the assumption that rotation is detrimental because visual-motor habits are continually being disrupted, because rotation will prevent the development of any such visual habits. Only one possibility remains,—the assumption that these visual alterations operate as distractions.

4. Vision is an advantage in the mastery of the maze, when the rats have had previous experience on other problems. The paucity of data upon which this conclusion is based renders its validity questionable. Accepting the fact at its face value, we may assume that the previous experience of the normal animals has operated to render them less dependent upon the extraneous environment; this result will minimize their susceptibility to the distractive influences of the rotation as demanded by the conclusion of the previous paragraph. The two groups thus approximate equality as to susceptibility to the distractions due to rotation, and the visual group is now enabled to master the maze more readily in virtue of its greater learning capacity.

All comparative data on the mastery of the maze can thus be explained on the assumption that vision possesses both detrimental and beneficial features in relation to the mastery of a maze problem. Visual stimuli tend to distract the animal and thus retard the development of the kinaesthetic-motor habit. The existence of vision on the other hand increases learning capacity. Two conceptions of the relation between vision and learning capacity receive some factual support. Light exerts a tonic and stimulative effect upon activity, while on the other hand the removal of the eye balls is to be regarded as some sort of a positive disturbing or distracting factor.

As to the nature of the process of adaptation, certain explanatory conceptions may be suggested. 1. We may suppose that the alterations disrupt the system of sensori-motor connections involved in running the maze, and that adaptation is to be conceived as a process of reorganization,—the acquisition of new motor controls. This conception assumes a directive function for the senses involved. Animals with vision have an advantage because they can utilize visual as well as other sensory cues.

2. The distractions and resulting errors induce confusion and excitement, and this confusion may now operate as a further distraction. Adaptation is a process of minimizing and allaying this excitement, and all familiar or unaltered stimuli will possess this quieting and reassuring characteristic. Adaptation is a matter of learning to direct the attention to the familiar aspects of the environment. Rats with vision will have an advantage because of their greater learning capacity and their greater sensory contact with the environment. 3. The disturbances are due to distracting stimuli, and adaptation is a process of strengthening the maze habit up to a point where it is immune to the distractive effects of those particular stimuli. Adaptation is thus a further process of learning, and those animals with the greater learning capacity will manifest the greater adaptive power. On this assumption the adaptive capacity of normal rats will be greater than that belonging to blind animals. 4. Blind rats are less resistant to distractions because of the operative effects. As previously noted, these effects may be conceived as intraorganic distractive stimuli of some sort, or as nervous conditions conducing to exaggerated and erratic responses. Blind rats will be regarded as essentially unstable organisms, subnormal in their capacity of resisting distracting stimuli. 5. Adaptation may be conceived as a process of decreasing sensory susceptibility to stimuli due to neural or end organ changes somewhat akin to fatigue. On this hypothesis any end organ can adapt only to those alterations which were sensed by that receptor.

The factual data are insufficient for any very confident judgments as to the relative validity of these various hypotheses. The normal animals manifested by far the greater adaptive power; this fact is readily explicable in terms of any one of the first four conceptions. The difference of adaptive capacity of the two groups is generally greater than their differences in learning ability as manifested in the mastery of the maze; this fact militates against the 1st and 3rd conceptions as complete explanations of adaptation. The first conception must be summarily dismissed as the facts indicate rather conclusively that extraneous stimuli do not function as motor controls after the maze is mastered. The greater variability of the blind rats may be explained on the basis of either the 2nd or the 4th hypotheses. The immunity to distractions due to adaptation is mainly specific rather than general; this fact eliminates the 3rd hypothesis as a complete explanation of the process, since rats in time should become practically immune to all ordinary distractions. Neither can the fact be readily envisaged under the 4th and 5th conceptions; it is most easily explicable in terms of the 2nd hypothesis. A sense organ can play a part in the process of adaptation although the disturbance was mediated through some other sense avenue. Normal rats displayed the greater adaptive power in the hunger experiment, so that vision must have been concerned in the process although the disturbing conditions were intraorganic. This fact would eliminate the 5th conception as a complete explanation of adaptation. The maximum adaptive power of normal rats was manifested in those experiments in which the optical features of the environment were altered. Adaptation was very rapid when either the maze or the environment was rotated in reference to each other, but no adaptation was present when both maze and environment were rotated simultaneously. This fact may be conceived in either of two ways: 1. We may assume that the eye can adapt only for visual distractions. This assumption naturally suggests the 5th conception. 2. We may assume the truth of the 2nd conception, and explain the inability of the normal rats to adapt to the rotation of maze and environment as due to the homogeneity of the visual environment in this experiment.

These conceptions are not mutually exclusive; all may contribute to the process of adaptation. Only the first possibility must be summarily dismissed. The second conception receives the most support, as there are no facts which can not be explained in its terms. The 3rd conception meets the greatest amount of difficulty; it can not account for the entire process of adaptation. The evidence for and against the 5th hypothesis is about equally balanced.

CONCLUSIONS

The white rat is sensitive to optical stimuli through the medium of the eye.

Both advantages and disadvantages accrue from the possession of visual receptors in the maze situation.

Vision is detrimental because of the distractive effect of retinal stimuli.

The advantageous features of vision may be explained in either of two ways: Retinal stimuli exert a tonic and stimulative effect upon organic activities and thus promote learning capacity, or one may assume that blind animals are at a disadvantage because of certain deleterious effects of the operation.

Vision may possess other functions in the maze situation; our facts are inconclusive on many points.

These conclusions apply merely to the situations obtaining in our experiments; other potentialities of vision may be realized in different types of situation.

MAZE STUDIES WITH THE WHITE RAT

III. Anosmic Animals

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Anosmic animals were employed to determine the function of olfaction in the environmental alterations described in the first paper. Records were secured from nine anosmic and five blind and anosmic rats. For these animals I am indebted to Miss Vincent. Professor Herrick made a histological examination of a group of seven of these defective rats. He reported that the operation was successful for two of the anosmic animals and for but one of the five blind and anosmics. From this record it is obvious that no conclusions drawn from the records of defective animals can be trusted without a subsequent histological examination. In our comparisons we shall utilize the data from the three animals of whose defective condition we are certain. Any conclusions from such a small group must necessarily be regarded with suspicion; however, we shall state the facts as they are and indicate their significance.

ANOSMIC ANIMALS

The anosmic operation exhibited no apparent deleterious effect upon the vitality of the animals. These animals were kept in the laboratory for nearly a year. Their appetite was undiminished; they looked sleek and well groomed, and the vigor and abundance of their activity was equal to that of normal animals.

One of the anosmic animals mastered the standard maze in two trials with a total error score of 40. The other rat required 21 trials and 127 errors to master the same maze. The average values for a group of 27 normal rats in mastering this maze were 18 trials and 144 errors. Evidently smell is not essential to the mastery of this type of maze. In this connection the construction of this maze must be considered; it was nearly water-tight and covered with closely fitting glass covers. Any olfactory contact with the extraneous environment must have been greatly minimized.

In the cleanliness test a single error was made by one animal in the first trial. A pronounced disturbance was manifested by members of the normal and blind groups of animals. Presumably, the alterations in this experiment were primarily olfactory in character. The facts indicate that these novel disturbing conditions are sensed wholly or mainly by means of smell.

The maze was learned with one side of the top open. This top was now removed. No disturbance resulted; neither were normal animals affected.

Both animals were affected by the rotation of the heterogeneous environment. Their average error record was 2.50 and errors were present in 75% of the trials. The disturbing effect was practically eliminated when the test was repeated. The average error score per rat for the first test was 15. These results are similar to those obtained for normal animals.

Both animals were slightly disturbed when both maze and environment were rotated. The average error record was but .42 and the errors were confined to one-third of the trials. The adaptive capacity of this group was not tested. These results are similar to those for normal animals with the exception of a smaller error score. Taken at their face value, the facts indicate that anosmic animals are less sensitive to these changes than are normal or blind rats.

Rotation of the uncovered maze disturbed both animals. Their error record for the first test was 5.08, and the disturbance was present in 83% of the trials. A repetition of the test reduced the above values to 1.00 and 60% respectively. For the first test the normal records were 6.95 and 65%, while the corresponding values for the second test were 1.72 and 47%. These results indicate that anosmic animals are slightly less sensitive to these changes than are normal rats.

Variations in the position of the living cage exerted a pronounced disturbance with one rat and a slight disturbance with the other. The average error record was 5.00 and errors were present in 75% of the trials. These rats were subjected to a 24-hr. exposure before being tested. The results indicate a greater susceptibility than that of either blind or normal animals; a corrective function must be ascribed to olfaction in this case.

The cage was first rotated for the three new positions on successive days. No disturbance was manifested. Both blinds and normals were disturbed in similar conditions. This fact would indicate a sensitive function for olfaction. The rats were now left in each new position for five days and tested daily. No effect was observable for the first position. In the second position both rats manifested considerable hesitancy and indecision in nearly every run and one rat made eleven errors in one trial. The hesitancy and indecision were again apparent for the third position; one rat made fourteen errors in two trials, and the other eleven errors in one trial. Prolonged exposure thus induces a disturbance. The fact again indicates a defective sensitivity on the part of these rats.

These two anosmic rats belonged to a group of three animals, one of which died before the series of tests were completed. The record of this rat which was not histologically examined was similar in every respect to those given above.

A group of six anosmics were subjected to several tests on the sideless maze in the early part of the experimentation; these were not examined. Their results, however, were similar to those two which are known to be anosmic. The degree of disturbance was practically identical with that for normal rats in the following experiments,—position of experimenter, position of maze, and rotation of maze. They exhibited little evidence of any disturbance when the cage was rotated or altered in position.

BLIND AND ANOSMIC ANIMALS

Five such animals were tested and afterwards examined. All were pronounced blind. The anosmic operation was completely successful in but one case. Both olfactory bulbs were intact with one animal; evidently the bulbulous material in front of the olfactory lobes had been removed in this animal. With two animals the left lobe had been successfully removed while the right lobe remained intact or partly severed. In the remaining animal the sections were made through the frontal lobes of the cerebral hemisphere; on one side the section was sufficient to destroy olfaction; on the other olfactory connections were still possible. This group of rats thus consists of one blind, one blind and anosmic, two blind and partially anosmic, and one which we may term a defective because of the loss of considerable cerebral tissue.

The learning records of this group of animals present many interesting features. The blind animal mastered the maze in 24 trials with a total error score of 152. After this time, the rat ran the maze consistently without error. This record is similar to those for blind and normal animals. Those two that were blind, and anosmic on the left side gave poorer records; one required 52 trials and 144 errors, and the second 102 trials and 508 errors. After the maze was mastered according to the criterion used, many errors kept appearing in an irregular manner for 25 to 40 trials. The blind and anosmic animal did still poorer; it required 130 trials and 2582 errors to learn this maze, but the act did not become thoroughly automatic until the 200th trial. It was also necessary to help this rat in 76 trials while learning the maze. In the early trials this animal utterly failed to reach the food box after several hours of effort and an error score of over 100. After the animal became exhausted I would stimulate it to further efforts and guide it when necessary. After the twentieth run I aided the rat whenever it became apparent that it was hopelessly lost. The defective rat required 194 trials and 1855 errors to master the maze. It was also helped in 32 of its trials. The act did not become thoroughly automatized for some time after the maze was considered learned. These results are significant because the difficulty of mastery is proportional to the degree of olfactory deficiency. The loss of either smell or vision does not operate as a detriment to the mastery of the maze; the loss of vision together with the partial or total destruction of smell is exceedingly detrimental. Evidently the deficiency due to the absence of either vision or smell is compensated in some manner by the other sense, while the remaining senses are unable to compensate for the deficiencies of both.

Rotation of the heterogeneous environment produced little disturbance upon the blind and anosmic or upon those which were blind and partially anosmic. The average error records for six trials were .33 and .66 respectively. The error record of the defective animal was 2.33. The normals gave a score of 1.90, the blinds 2.32, and the anosmics 2.50. Evidently the loss of both senses minimizes or practically abolishes the rat's sensitivity to these changes.

Uncovering the maze produced no effect. Neither was a disturbance manifested by the normals or the anosmics.

In the cleanliness test the blind and anosmic made 14 errors in one of its trials. Those which were blind and partially anosmic gave an error record of .50. These animals exhibited about the same degree of sensitivity as the anosmics. Their sensitivity was much less than that of either the normals or blinds.

Only one blind and partially anosmic animal was subjected to a rotation of maze and environment; its error record for six trials was 4.16, which is greater than those for normals or anosmics, but less than that for the blind rats.

The blind and anosmic was not affected by a rotation of the maze. A blind and partially anosmic rat gave an error score of 2.50, which is less than that for either anosmics, normals or blinds.

The blind and anosmic animal was not affected by changes in the position of the maze. The two which were blind and partially anosmic gave an error record of .75 which is less than that for any of the other sensory groups.

The blind and anosmic rat was disturbed by a rotation of the cage only after a considerable period of exposure to the novel situation. Errors were present in three of fourteen trials. The average error record was .78. The degree of sensitivity was about the same as that for the anosmics. The two blind and partially anosmic animals were more susceptible; their error record was 1.68 for eighteen trials. These animals were disturbed less than either the blind or normal groups.

A significant feature of these results is the practical insensitivity of the blind and anosmic rat to all alterations instituted after the mastery of the maze. A total of 50 trials was given, of which 80% were without error. The average error record for the 50 trials was 1.50. In the previous 50 runs, errors were absent in but 59% of the trials and the average error record was 2.70. This animal made a better record during the tests than during the later stages of increasing automaticity and after the maze was considered mastered. No errors were present in the first four experiments involving a total of 24 trials. The first indication of a disturbance was manifested in the fifth experiment in which the cage was rotated; a total of 11 errors was made in three of the 14 trials. The sixth test involved the cleansing of the maze, and 14 errors occurred in the first trial. After the regular series of tests were completed, both cage and maze were rotated simultaneously in the hope of inducing more serious effects; error scores of 40, 5, and 1 were secured in three of the 10 trials. Rotation of cage and cleansing the maze were the only tests which induced disturbances, and it is possible that these results may have been due to chance irregularities. Granted the validity of the results, the question arises as to the sense avenue through which the changes were instituted. The changes resulting from cleansing the maze may well have been perceived through the sense of contact, for undoubtedly the contact values of the bottom of the runways were altered. Rotation of the cage may have affected the animal by means of its sensitivity to heat as the cage was located in the proximity of a steam radiator.

The practical insensitivity of the blind and anosmic animal considered in conjunction with the sensitivity of all other groups including those animals which were blind and partially anosmic indicates that all of these alterations are sensed almost wholly through smell and vision. This conclusion does not warrant the assumption that the rat does not possess any other efficient avenues of sensitivity. The statement merely means that smell and vision are the only senses adapted to the detection of these particular alterations of the environment.

Since vision and smell are the only effective senses in our conditions, it follows that all disturbances manifested by the anosmic group must have been instituted by means of vision, and that we can utilize the data of this group in determining the function of vision. This hypothesis is supported by the facts, for the results are in harmony with the conclusions as to the function of vision previously derived from the differential records of the blind and normal animals. All experiments involving an alteration of the optical environment were very effective upon the anosmic animals; this group of tests comprised rotation of environment, rotation of uncovered maze, and a change in the position of the living cage. On the other hand those experiments involving a minimal optical element, such as cleansing the maze and rotation of the covered maze, had little effect upon this group of rats. Moreover, the anosmic group when disturbed exhibited powers of adaptability on a par with normal animals. This adaptive capacity was in evidence in the experiments in which the environment was rotated in reference to the maze, or the maze was rotated in relation to the environment. The records of these anosmic animals thus confirm our previous conclusion as to the sensitive and corrective values of vision.

The function of smell may be determined from several sources. 1. Since no other senses than smell and vision are concerned in these tests, the records of the blind rats must be due exclusively to the olfactory factor. 2. The differential sensitivity of the blinds as compared with those blind and partially anosmic must be interpreted in terms of smell. 3. The records of the normals as compared with those of the anosmic group must likewise be explained in terms of smell.

Smell possesses a sensitive function; by this statement we mean that these alterations do affect in some way the animal's behavior through the medium of olfaction. All three sets of facts support this conclusion. The blind and partially anosmic group suffered less disturbance than the blind rats in every experiment in which comparisons are possible. The anosmics on the whole manifested a lesser degree of sensitivity than did the normal animals; their sensitivity was much less for those experiments, e.g., cleanliness test, in which the olfactory element predominated. The blind animals, possessing only smell, exhibited the maximum amount of disturbance in those experiments in which the anosmic animals were the least sensitive. In the cleanliness test, those animals with smell intact,—blind and normal groups, suffered a pronounced disturbance, while but little effect was manifested by those groups in which olfaction was partly or completely eliminated.

In the previous paper, we noted that blind rats were sensitive to alterations of the environment, and concluded that these alterations operated as distractive stimuli rather than as motor controls. The results of this paper prove that smell is the main mediating sense involved in the detection of these changes by blind rats. No additional facts were developed necessitating a revision of the conclusion as to the distractive character of these olfactory stimuli.

Several significant features are contributed by the experiments concerning the functions of smell and vision in the mastery of the maze. Anosmic animals learn the maze as readily as do normal rats. The olfactory operation produces no deleterious effect upon the vitality or behavior of the animals. The elimination of vision slightly decreases learning capacity, but this effect is limited to certain individuals; the vital capacity of certain rats is also lowered. The combined loss of smell and vision exerts some effect upon vitality, but this effect is apparently no greater than that resulting from the loss of vision alone. The combined loss of the two senses results in a pronounced decrease in learning capacity, an effect which can not be regarded as the arithmetical sum of the results of the two operations taken separately.

These facts indicate that the diminished vitality and learning capacity of the blind animals and the blind and anosmic groups can not be due to any effects of the operation *per se*, such as surgical shock, ether effects, etc. The anosmic operation is much more serious and difficult than the optic one, and any operative effects should be more evident and more extensive in the anosmic than in the blind groups. The reverse situation obtained; the anosmics were not affected while many of the blind rats were. The combined operation for the two senses is not any more prolonged or severe than for smell alone. If the operative effects are responsible for the deficiencies of learning capacity, one should expect as good records from the blind and anosmic groups as from the anosmic animals; as a matter of fact the anosmic animals suffered no deleterious effects while the learning capacity of the blind and anosmic rats was far below normal.

In the previous paper we noted three possible ways in which any sense might function in order to increase learning capacity. Sensitivity may be advantageous because of either a directive or tonic influence upon behavior and the vital activities. The removal of a sense organ may be disadvantageous not because of the elimination of sensitivity but because of certain deleterious effects of the operation itself. The directive function of vision for our conditions was decisively eliminated as one of the possibilities. The data of this paper also eliminates the third hypothesis. We are thus forced to conclude that the beneficial influence of vision upon learning capacity is due to the tonic and stimulative effect of retinal stimuli.

Similar possibilities obtain for the function of smell in the acquisition of the maze habit. The facts previously given exclude the hypothesis of operative effects for smell as well as for vision. As between the directive and tonic hypotheses no confident decision can be made. The records of the blind rats indicate that smell exerts no directive function after the maze is learned, but it is possible that olfactory controls may be utilized in the formation of the habit and yet be noneffective after the maze is mastered. The functions of smell and vision compensate for each other in the learning process. This fact is most easily interpreted on the basis that both senses have the same function. Since vision is efficacious because of its tonic effect, we would need to assume the same function for smell. On this hypothesis, a certain amount of sensory stimulation is necessary to induce sufficient motor activity requisite for learning. This effect can be secured through either smell or vision, while the elimination of both senses is disastrous. However, it is not entirely impossible to conceive that the two senses may compensate for each other even though their functions are different. One may suppose that vision exerts a tonic effect while the function of smell is that of control. There is good evidence that control is secured mainly through the medium of the cutaneous and kinaesthetic senses. One may now suppose that the cutaneous and kinaesthetic control requires a certain amount of supplementation and that this effect may be furnished by either the tonic function of vision or the additional control exerted by smell. A final fact supports the tonic hypothesis for both smell and vision. The blind and anosmic animals differed from the other groups in that they lacked persistence, initiative and incentive. I refer to the fact that these animals required help or additional stimulation in many of their trials. One possible interpretation of this fact is obvious; we may assume that these animals lacked a sufficient amount of sensory stimulation to arouse the motor activity adequate to the situation. Their activity was deficient in vigor, decisiveness, and persistence. These animals possessed the normal amount of energy, and the proper kind of stimuli for the control and direction of this energy, but they were so deficient in their sensory capacity that an adequate amount of this potential energy was not released. Additional stimuli of an auditory or cutaneous character were requisite to overcome this deficiency.

The comparative data confirm our previous conclusion that the eye possesses some peculiar adaptive capacity. The adaptive power of anosmic animals is practically equal to that of the normals, while the capacity of both groups is much superior to that of the blind animals. The superiority of one group over another is thus not a matter of the number of senses, but rather of the kind of sense involved. Adaptation can not be conceived as a pure process of learning, since the blind and partially anosmic animals appeared to adapt as readily as did the blind rats although their learning capacity is much inferior. Neither can the differences in adaptive capacity of the various groups be due to operative effects, for on this hypothesis the adaptive ability of the anosmics should be inferior to that of the blind animals.

There is no conclusive evidence that smell is concerned in the process of adaptation. Although the blind rats did adapt to the distractive influences of olfactory alterations, it is entirely possible that this effect was mediated through the kinaesthetic-motor processes. There is some evidence that the distractions mediated through one sense can be corrected for through another. If smell is concerned in any overt manner in the process of adaptation, one would expect the adaptive power of normal animals to be greater than that of anosmic rats. Likewise blind rats should manifest greater ability than that possessed by blind and partially anosmic animals. There are no facts which indicate in any conclusive fashion the truth of either of these suppositions.

CONCLUSIONS

The results of this series of experiments confirm the conclusions of other investigators that the maze habit consists essentially of a tactual-kinaesthetic motor coordination.

This act is dependent, nevertheless, both during and subsequent to its development upon a wider sensory situation of which it is a part. This fact was proven by an experimental control of the relation between the animal and the environment.

The sensory connection between the act and those aspects of the environment which were altered was mediated almost exclusively through vision and smell.

The development of the act is contingent upon retinal impulses in two ways. On the one hand, retinal impulses operate as distractions, tending to prevent and delay the final perfection of the coordination. This distractive effect is present even when the relation of the visual environment to the rat remains stable. Any alteration of the environment from trial to trial increases the distractive effect. On the other hand, these retinal impulses tend to promote or condition the organization of the component elements of the act in so far as these impulses arouse the motor activity requisite to the solution of the problem. There are several ways of conceiving of this relation between visual stimuli and increased learning capacity. The experiment furnished no data for a choice between the several possibilities.

The development of the act is also dependent upon olfactory stimuli. No facts are pertinent as to the distractive or detrimental effect of these stimuli. Olfactory impulses, however, aid in the development of the act. These stimuli may be utilized as controls, or one may suppose that they are advantageous because of their tonic effect upon the various activities involved in the process of learning. No confident decision can be made as between these alternatives, though the latter hypothesis receives the greater support from the relevant data.

The act is still dependent upon these visual and olfactory stimuli after it has become thoroughly automatized, provided it was developed while these stimuli were present. The act can be acquired and function successfully when these stimuli have been completely eliminated. When the act was acquired while these stimuli were present, it will still function successfully when they are subtracted at least in part, or so long as their positional relations to the organism remain unaltered. Any positional change of these stimuli or the addition of new elements operate to disrupt or interfere temporarily with the successful functioning of the act. These changes of the stimuli function as distractions; they release impulses which the organism is unable to integrate successfully into the series of motor activities. The act is temporarily disrupted or disorganized.

Some degree of adaptation to these disturbances is the rule for all sensory groups. The experiments furnished no data which prove that smell is concerned in the process of adaptation. Vision certainly possesses an adaptive function. Of the five suggested hypotheses as to the relation between vision and adaptation, two are disproven by the experimental data. Three possibilities remain. Adaptation may be a further process of automatization and rats with vision are at an advantage because of their greater learning capacity. Adaptation can not be explained wholly in terms of this conception as the adaptive capacity of the various groups of animals is not proportional to their relative learning ability. Visual adaptation may be a process of decreasing sensory susceptibility to the distractive stimuli. This conception can not wholly explain the phenomenon as certain facts indicate that vision can correct for disturbances mediated through other sensory avenues. Unaltered or familiar visual stimuli exert a quieting and reassuring effect upon the organism and enable it to resist the distractive effects of other stimuli. There are no facts which can not be explained fairly successfully on the basis of this hypothesis.

The maze act and the learning process are much more complicated phenomena than the conclusions of some previous investigators would indicate. The habit does not consist merely of tactual, kinaesthetic and motor elements. Other accessory and conditioning components are also present. Learning does not consist merely of the organization of certain tactual and kinaesthetic stimuli with certain movements. Many other sensory factors are present which release their quota of impulses that must be harmoniously integrated and organized in some fashion adapted to the solution of the problem.

All statements as to the functions of smell, vision, or other senses must be interpreted as applying only to the situations obtaining in these experiments.

NOTES ON THE MIGRATION OF THE HESSIAN FLY LARVAE[1]

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The migration of the Hessian fly (*Mayetiola destructor* Say) larva on the leaf where it hatches to its feeding place between the leaf-sheath and the stem is one of the most critical periods in the life history of the insect, yet the literature on this point in the life economy is very meager. Packard (1883, p. 213) makes the following statement: "as soon as the footless larva or maggot hatches, it makes its way down the leaf to the base of the sheath." Osborn (1898), Thorne (1902), Felt (1902), Webster (1906 and 1915), Forbes (1910) and many others simply recapitulate the brief statement quoted from Packard.

Enock (1891, pp. 333-334) made some interesting observations on this point. He states that "the female fly, as a rule, lays her eggs with the head end pointing downwards towards the main stem, so that when the tiny larva emerges it is started from its infancy in the right direction on its journey downwards, and, guided by the longitudinal striae of the leaves, it reaches the stem, round which the leaf-sheath is closely wrapped, but not too close to prevent the larva forcing its way; until, after some four hours' steady travelling (during which time it has covered only the small distance of two or three inches), it reaches the base of the sheath." He also made some observations on the hatching of eggs that were laid " the *wrong* way, with the heads towards the *tip* of the leaf." In this case, " the larvae worked their way to the tip of the leaf, where some of them managed to cross the edge and get on to the back or under side, and commenced their tremendous journey of four or six inches ! some arriving at their destination at the next joint *below* the one they would have occupied had the female laid her eggs on the inside of the upright leaf."

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[1] Contribution from the Entomological Laboratory, Kansas State Agricultural College, No. 26. This paper embodies the results of some of the investigations undertaken by the authors in the prosecution of project No. 8, Kansas Agricultural Experiment Station.

Garman (1903, pp. 221-222) reports that " the eggs hatch in a week or less (three days in one instance observed), according to temperature, and begin their rather laborious journey to the leaf-sheath, during which they find even an egg or egg-shell an obstruction to be surmounted with difficulty. From the slowness of their progress the trip requires hours of time, and excepting as their minute size protects them, they are completely at the mercy of enemies. No doubt many of them are lost at this period of their lives." The same author states (p. 221) that when the eggs are laid on the lower surface of the leaf " the helpless young must have difficulty in finding their way between the leaf-sheath and the stem, with a good chance of perishing before this is accomplished, since it is their habit to follow closely the grooves in which they hatch down to the junction of blade with stem."

Gossard and Houser (1906, p. 4) report that the young larva " starts at once down the leaf, following the groove or crease in which it hatched, or an adjacent one, until it reaches the base; from this point it burrows between the leaf sheath and the stalk until it reaches the foot of the culm, . . . While on this downward journey, which may occupy several hours, the young larva is easily deflected from its course by dirt particles or mechanical obstructions, and may lose its hold and fall to the ground, or may die, and in dried and shriveled condition remain for a time on the leaf." After performing some experiments to see if the larva could follow the creases of the blades up an incline, if it were necessary for the larvae to do this, in order to reach the base of the culm, they state (p. 5.) that "in no instance did a larva make more than a slight advance upward, and most of them died with their bodies extended crosswise of the creases, near the points where they had hatched." They add that the bearing of this experiment on the following statement quoted by Packard (1883, p. 212) is readily apprehended: "A reason given by some why the fly does not injure red wheat as much as white, is because the leaf of the red grows so long and slants down from the shoot, so when the egg hatches, the maggot works down the wrong way, falls to the ground, and so many fail to harm the wheat."

Headlee and Parker (1913, pp. 95-96) state that the larva "seems to have various means of getting down into the plant; some observations made by Mr. Kelly would indicate that in the presence of abundant dew it is washed down by the droplets of water. In other cases it undoubtedly crawls down, earthworm-like, following the groove until it reaches the place where the leaf-sheath winds tightly about the stem. Get down as it may, when once there it squeezes in between the leaf-sheath and the main stem and continues its way downward until it nearly reaches the point where the leaf takes its origin. Just above this point it stops and begins to feed."

METHODS OF STUDY

The experiments on which this paper is based were carried on in the breeding chambers of the air conditioning machine described by Dean and Nabours (1915). The temperature was maintained at approximately 70° and the humidity at about 70%. The wheat plants were grown in wide-mouth bottles containing Pfeffer's liquid plant food solution.[2] The roots of

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[2] Pfeffer's solution for wheat cultures is prepared as follows:

Calcium nitrate	4 grams
Potassium nitrate	1 gram
Magnesium sulphate	1 gram
Potassium dihydrogen phosphate	1 gram
Potassium chloride	0.5 gram
Ferric chloride	Trace
Distilled water	5 liters

the plants were kept in the liquid while the remainder of the plant was outside the bottle. The plants were held in place with a cotton stopper in the mouth of the bottle. This method proved very satisfactory because of the fact that the plants could be handled conveniently and the various stages of the fly could be studied with greater ease and exactness than when the plants were grown in soil.

OBSERVATIONS

Eggs.—The egg of the Hessian fly is very minute, being only about 0.5 mm. in length, cylindrical, obtusely rounded at the ends, glossy, translucent and pale yellowish red. This color deepens with the development so that just before hatching it is distinctly reddish in color. About the second day after deposition the posterior end of the egg becomes opaque, and shows no reddish content. This is very characteristic of the fertilized egg. The caudal extremity of the embryo is located in this end of the egg. Generally, the eggs are laid on the upper surface of the leaf, being glued into the longitudinal creases of the leaf-blade. Frequently the eggs are laid on the lower side of the blades of wheat plants, and occasionally on the stalk.

Hatching of Eggs.—The majority of eggs hatched in about 60 to 72 hours after deposition under the experimental conditions of the breeding chamber where the mean temperature was 70° F. and the mean relative humidity 70%. The exact method whereby the hatching occurs is not as yet ascertained. The egg-shell seems to split along its cephalo-dorsal aspect and the larva emerges quickly. Enock (1891, p. 333) records some observations on the hatching of the eggs. He found that the movements of the inclosed larvae could be distinctly seen on the third day and on the fourth day he was able to distinguish the muscular efforts of the larvae to burst open the shell, which they succeeded in doing after three or four hours work.

Orientation of the Larva.—Immediately after emerging from the shell, often before the body is more than one-half out of the egg-shell, the larva begins to turn sidewise, describing an arc and finally orients itself in the direction exactly opposite to that in which it had been within the egg (Fig. 1). This orientation behavior was first noticed when larvae, hatching from the eggs laid by a female held in an inverted position on the leaf during oviposition, instead of moving down toward the base of the leaf as the larvae were ordinarily known to do, moved up toward the tip of the leaf. In order to see if this seemingly abnormal behavior was merely accidental or really of regular occurrence, the following experiment was performed:

A young wheat plant was held in an inverted position and a female was allowed to oviposit on it. After the eggs were laid, the plant was turned right side up and kept under observation for the hatching of the eggs. Emergence occurred on the third day and the larvae turned away from the base of the leaf and moved up toward the tip of the leaf. This simple experiment was repeated a number of times and the result was always the same. Then the test was made with a number of modifications. In the first place, the influence of the orientation of the egg itself on the subsequent orientation of the larva was to be tested. In order to do this, it was necessary to have the eggs laid in as wide a variety of ways as possible, keeping in mind the possibility of such occurrence out in nature. Barring the minor modifications, there are three distinct ways in which eggs may be laid: (1) The eggs may be laid with their anterior end pointing toward the tip of the leaf. This is what happens in normal situations when the female stands on the leaf with her head toward the tip of the latter. Since this mode of oviposition by Hessian fly is the most general out in nature, and since this is the most natural way of ovipositing under ordinary circumstances, it will be designated in this paper as normal. (2) The eggs may be laid with their anterior end toward the base of the leaf. This is the situation exactly opposite to that of the first, and, undoubtedly, is of rare occurrence in nature. Only under forced conditions, and then with difficulty, will the female attempt to lay eggs while in an inverted position. Many such

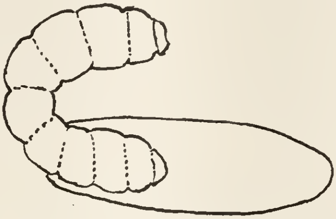

FIG. 1.—Hessian fly larva hatching from egg and turning toward posterior end.

attempts fail to bring about actual oviposition. The artificial method whereby the inverted eggs may be secured has been already described. The same result may be realized when the leaf is long and bends over, and the female alights beyond the bend with her head towards its base The base in this situation will be higher than the tip of the leaf. This mode of oviposition and the orientation of the egg will be here designated as inverted. (3) The eggs may be laid transversely or at varying angles with the long axis of the leaf. It is only necessary to mention that the three conditions described above are capable of modifications and also that they can be realized on the lower as well as on the upper surface of the leaf.

A series of experiments with eggs laid according to the methods stated above were performed, in connection with which more than three hundred larvae were studied and their behavior recorded. In no instance was the orientation of the larvae, soon after hatching, not in accordance with the expectation. Every one of the three hundred and more larvae turned towards the caudal end of the egg regardless of the manner of oviposition, position on the leaf, and in cases of inverted oviposition, regardless of the fact that this orientation leads the larvae away from the only possible feeding place, namely, the base of the leaf-sheath.

Migration of Larva on the Leaf.—The direction of movement, as has been stated, is predetermined by the orientation of the egg itself, and is not in any way influenced by the condition of the leaf upon which it is laid. After the initial orientation, the larva usually starts without delay on the journey down the leaf, following the first or second grooves adjacent to the one in which the egg was located. The movement is subject to variation in regard to the rate of progress, although generally it is a slow process. The larva may move continuously or it may rest now and then. When it reaches the base of the leaf or the ligule, it crawls up the latter, squeezes in between the leaf-sheath and the main stem, and continues its way downward to a point just above the joint or origin of the culm. In the case of inverted oviposition, the larva, on hatching, turns toward the tip of the leaf and this is the direction of its progress It works its way slowly up the leaf, against the force of gravity, and constantly subjecting itself to danger of various sorts. When it reaches the tip of the leaf, it stops and apparently surveys the ground for a while, then getting by chance into another groove, it starts downward. Once on this course it works its way down in the same manner as the larva which came from an egg deposited in the normal manner. The behavior of the larvae hatched on the lower surface of the leaf is essentially similar to that of those on the upper surface. There was a tendency among the larvae from eggs laid in an inverted position on the lower surface to get over to the upper surface after they have gone up the leaf for some distance.

Rate of Migration.—Individual differences influence the rate of migration more than physical factors, such as the degree of inclination of the leaf, temperature, humidity, mechanical obstructions, and the like, although these factors always enter into the problem and need to be taken into consideration. The larvae which came from eggs laid in succession by the same female on the same leaf and in juxtaposition may not be able to move at the same speed. As a matter of fact, none of the larvae under observation moved according to any set of arbitrary standards. Tables I and II show the rates of migration of larvae when the eggs are deposited normally and when they are deposited in an inverted position.

TABLE I

RATE OF MIGRATION OF LARVAE HATCHED FROM EGGS LAID IN NORMAL MANNER

		Average time required to move 1 mm.	Average distance traveled
Total No. of larvae............	205	4 min. 36.4 sec.	51.5 mm.
No. of larvae that got down into sheath.................	157	4 min. 1.6 sec.	53.3 mm.
No. of larvae died on leaf......	48	6 min. 30.6 sec.	45.5 mm.

TABLE II

RATE OF MIGRATION OF LARVAE HATCHED FROM EGGS LAID IN INVERTED POSITION

		Average time required to move 1 mm.	Average distance traveled
Total No. of larvae............	119	3 min. 38.7 sec.	99.3 mm.
No. of larvae that got down into sheath.................	51	2 min. 11.2 sec.	144.9 mm.
No. of larvae that died on leaf..	68	4 min. 44.3 sec.	65.1 mm.

It is interesting to note that larvae hatched from eggs laid in inverted position, not only traveled longer distances on an average but traveled at greater rates than those that hatched from eggs laid in normal position. Table III is a comparison of the rate of migration up the leaf with the rate of migration down the leaf when the eggs are laid in an inverted position.

TABLE III

Comparison of Upward Migration with Downward Migration. Eggs Laid in an Inverted Position

		Average time required to move 1 mm.	Average distance traveled
Upward Journey—			
Total No. of larvae	30	3 min. 43 sec.	50.1 mm.
No. of larvae that got down into sheath	18	4 min. 29.2 sec.	38.0 mm.
No. of larvae that died on leaf	12	2 min. 35.3 sec.	70.2 mm.
Downward Journey—			
Total No. of larvae	12	3 min. 55.8 sec.	88.1 mm.
No. of larvae that got down into sheath	11	4 min. 10.5 sec.	89.5 mm.
No. of larvae that died on leaf	1	1 min. 38.0 sec.	73.0 mm.

Thus, as the table indicates, there seems to be no marked difference in the rate of progress during the journey in either direction, that is, the larvae, on an average, move with equal facility on either an ascending or descending incline.

Table IV is appended in order to give a little more accurate notion of the migratory rate, since these larvae were under closer observation.

TABLE IV

Rate of Migration of Twelve Selected Larvae Hatched from Eggs Laid in an Inverted Position

	Upward Journey		Downward Journey		Entire Journey	
Larva No.	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled
	sec.	mm.	sec.	mm.	sec.	mm.
33-3	203	13	561	141	537	154
64-1	323	39	56	95	133	134
64-2	389	37	757	95	654	132
65-5	257	56	136	101	171	157
71-1	88	41	296	85	228	126
76-2	128	56	216	83	181	139

TABLE IV—*Continued*

	sec.	mm.	sec.	mm.	sec.	mm.
162-1	218	33	68	75	97	108
162-2	218	33	112	75	144	108
162-3	225	32	195	75	201	107
163-2	263	41	157	80	203	121
163-3	83	43	202	80	161	123
Average for 11 larva that reached the sheath	217.7	38.5	247.8	89.5	246.3	131.9
Larva that died on leaf	291	37	98	73	164	110
Average for 12 selected larvae	223.8	38.4	235.3	88.1	231.1	130.1

It may be of interest to note that there seems to be, as the preceding tables indicate, no correlation between the rate of migration and the distance traveled by the larvae resulting from two types of oviposition or between those larvae which died on the leaf and those that successfully reached the base of the plant. The maximum and minimum rates of migration when eggs are laid normally and when they are deposited in an inverted position are shown in Tables V and VI. Part 1 of each table gives the maximum and minimum average rates of migration with the distance traveled, while part 2 shows the maximum and minimum distance traveled.

TABLE V

MAXIMUM AND MINIMUM RATES OF MIGRATION OF LARVAE WHEN EGGS ARE LAID IN NORMAL MANNER

PART 1.—Maximum and minimum average rates of migration and distances traveled at these rates:

	Larva No.	Average time required to move 1 mm.	Distance traveled
Larvae that got down into sheath	231-1 Max.	27 sec.	131 mm.
	276-1 Min.	1800 sec.	2 mm.
Larvae that died on leaf	241-1 Max.	94 sec.	38 mm.
	277-4 Min.	4500 sec.	8 mm.

PART 2.—Maximum and minimum distances and rates of migration used to travel these distances:

	Larva No.	Average time required to move 1 mm.	Distance traveled
Larvae that got down into sheath	270-1 Max.	533 sec	162 mm.
	276-1 Min.	1800 sec.	2 mm.
Larvae that died on leaf	265-3 Max.	43 sec	84 mm.
	250-2 Min.	900 sec.	4 mm.

TABLE VI

Maximum and Minimum Rates of Migration of Larvae Hatched from Eggs Laid in Inverted Position

Part 1.—Maximum and minimum average rates of migration and distance traveled at these rates.

	Entire Journey		Upward Journey		Downward Journey	
	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled
Larvae that got down into sheath—						
No. 208-1 Max.....	24 sec.	294 mm.	?	139 mm.	?	155 mm.
No. 64-2 Min.....	654 sec.	132 mm.	389 sec.	37 mm.	757 sec.	95 mm.
Larvae that died on leaf—						
No. 221-1 Max.....	41 sec.	131 mm.	?	44 mm.	?	87 mm.
No. 226-1 Min.....	2769 sec.	26 mm.	?	26 mm.	0	0

Part 2.—Maximum and minimum distances and average rates of migration used to travel these distances:

	Entire Journey		Upward Journey		Downward Journey	
	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled
Larvae that got down into sheath—						
No. 208-1 Max.....	24 sec.	294 mm.	?	139 mm.	?	155 mm.
No. 70-1 Min.....	72 sec.	100 mm.	?	20 mm.	?	80 mm.
Larvae that died on leaf—						
No. 217-3 Max.....	46 sec.	158 mm.	?	98 mm.	?	60 mm.
No. 236-1 Min.....	300 sec.	12 mm.	300 sec.	12 mm.	0	0

According to Table IV, which records the behavior of 12 selected individuals which came from eggs laid in inverted position, there is absolutely no correlation of any sort between either the maximum or minimum speed and distance or maximum or minimum distance and speed. But Tables V and VI indicate that there seems to exist, so far as these particular individuals are concerned (although the same conditions apparently hold true in a number of other cases) certain correlations between the two items under consideration. The larvae which moved fastest traveled longer distances than those that moved slowest, and the larvae that traveled the longest distances moved faster than those that traveled the shortest distances. The rate of migration either on the upward or downward course, or on the upper or the lower surface of the leaf does not seem to be affected to any marked extent by the degree of inclination of the leaf. The leaf may have an inclination of anywhere between zero and 90 degrees, but the larvae seem to be able to move with equal facility in either direction. Acceleration or retardation, if any, due to the inclination of the leaf, usually is not appreciable; and even if it were of appreciable magnitude, it is better interpreted in terms of individual differences rather than due directly to any difference in the inclination of the leaf.

Variations in the Rate of Migration.—Every larva has a more or less different average speed from any other larva. Each larva has different speeds at different stages of migration. This variation in rate of migration in individual larvae can be seen in figures 2 and 3.

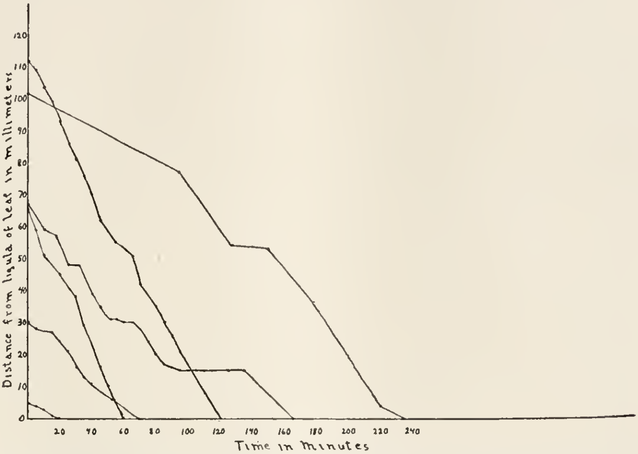

FIG. 2.—Chart showing the distance traveled and the rate of migration of six larvae hatching from eggs laid in the normal position. The dots indicate the location of the larvae at the time of observation.

As is shown in the figures, there seems to exist no regularity in the rate of progress in individual larvae. They may move faster at the beginning or toward the end of migration, or they may move fastest at the middle of the journey. Again, they may move for some time and then rest for an interval of from five or ten minutes to twelve hours or more.

Behavior of the Larvae on Migration.—The exact manner of the locomotion of the larva is hard to observe because of the minute size and the opaqueness of the wheat leaf. The larva seems to move in somewhat the same fashion as other footless insect larvae. The muscle tension coupled with the moist integument bearing intersegmented grooves and the rather rough, hairy condition of the creases of the leaf seem to operate in assisting the propulsion of the body of the larva. The process of orientation following hatching usually places the larva in a groove within the radius of the length of the body, which may be the first or second groove from the one in which the egg was laid. Once in a groove, the larva follows it down or up, as the case may be, until it reaches the end of the chosen path. In the case of normal deposition, this is the base of the blade where the short erect ligule which surrounds the stem arises. The ligule is a barrier which every larva must overcome, either by crawling over, as the majority of the larvae seem to do, or by avoiding it entirely by finding elsewhere a point of entry beneath the leaf-sheath. The larva, under favorable conditions, such as a clean, smooth ligule which is loosely wound around the stem, gets between the sheath and the stalk in a comparative short time. When the conditions are adverse, such as dirty, hairy, tight-fitting ligule and dry weather, the larva finds it extremely difficult to surmount the barrier and, in many cases, death overtakes it at this point, the usual mortality at this situation under experimental conditions being about 25%. The locomotion of the larva after it gets below the ligule has not been studied. When the larva, directed by the initial process of orientation, moves upward and reaches the tip of the

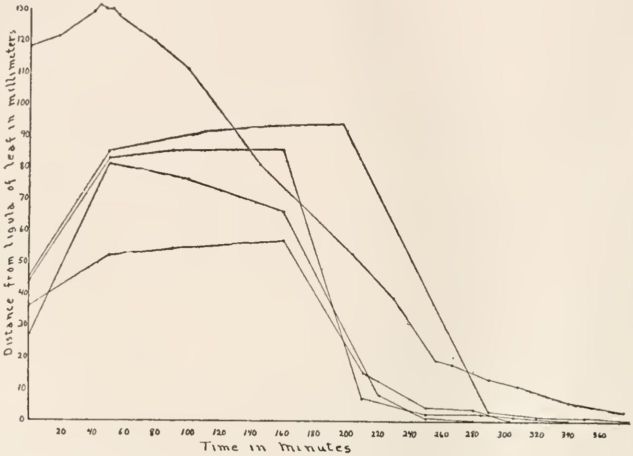

FIG. 3.—Chart showing the distance traveled and the rate of migration of five larvae hatching from eggs laid in an inverted position. The dots indicate the location of the larvae at the time of observation.

leaf where the grooves converge into a point at the extremity of the blade, it is then thrown upon its own resources in finding its way. It naturally performs random movements and in so doing it is likely to place itself now in inverted position in one of the grooves. This opens a way for the larva to escape the distracting maze of the tip of a leaf, and, after adjusting itself to the groove, it starts back down the long way it has so laboriously climbed up.

Variations in Behavior.—Although the larva is not known to refuse to turn round away from the direction of the anterior end of the egg, it may show individual differences or deviations from the ordinary course of behavior during migration on the leaf. Occasionally, a larva is found to cross the leaf-blade from one surface to another. This may happen at any point on the leaf but it usually takes place at or near the tip where the larva is forced to find a new way by random movements. When a larva meets an obstacle, e.g., a dirt particle, it usually seeks to avoid it by moving to an adjacent groove. Sometimes it may overcome the difficulty by actually crawling over the obstacle, or it may be forced to carry the impediment on its back, if the object is light enough to be lifted or pushed along. Small drops of water may wash the larva down away from the plant. A very small amount of water is found to be sufficient to trap the larva which loses it hold, and in case of a droplet, the maggot is not able to overcome the surface tension and free itself from watery imprisonment. It is not known whether the larva is capable of feeding on the leaf while migrating, although it seems to be the general feeling among the entomologists that it does not feed during this time. Enock (1891, 9, 334), however, states, that "the larva increases in width even before it disappears out of sight, leading one to suppose that it imbibes moisture as it journeys down the furrows of the leaf." Several cases of reversal of the direction of migration without apparent causes were noticed. In one case the larva, hatching from an egg laid on the lower side of the leaf, passed down to the stalk near the point where the latter passed into the culture solution. The larva turned around and started upward on the stalk which was standing vertically. After moving about 20 mm. the larva again reversed its direction of progress and started downward. In other cases, larvae were found to climb up the central stalk instead of crawling down into the culm. It is interesting to note that the larva seems to be unable to distinguish the right direction from the wrong when deflected from the former; e.g., larva 270-3, while moving down, was overtaken by larva 270-4, which forced it into the adjacent groove. The larva 270-3 was inverted completely by this treatment and when it started on its way was moving toward the tip of the leaf. This one died after moving 30 mm.

Mortality of Larvae on Migration.—The larvae, during their migration on the leaf, are in the critical period of their life and it is probable that many of them die. That such is the case is shown in Table VII, which gives the percentage of mortality of larvae from both normal and inverted eggs. Table VIII gives the details of the 68 larvae which hatched from the eggs laid in inverted position and which died on the leaf during migration. It is interesting to note that 53% of these larvae failed to reach the tip of the leaf. It is well to note, however, that these larvae had traveled the average distance of 56.6 mm. before they died.

TABLE VII

Mortality of Migrating Larvae

	Total No.	Larvae that got down into sheath	Larvae that died on leaf	Mortality, %
Larvae from eggs laid normal........	205	157	48	23.4
Larvae from eggs laid inverted.......	119	51	68	57.1
Total........................	324	208	116	32.7

TABLE VIII

Analysis of the Mortality of 68 Larvae that Hatched from Eggs Laid in an Inverted Position

	Total No.	No. of larvae died on upward migration	No. of larvae died on tip of leaf	No. of larvae died on downward migration
Larvae from inverted eggs that died on leaf	68	36	8	24
Percentage......................	100	53.0	11.7	35.3

Influence of Moisture.—The larvae seem to prefer moist air. Enock (1891, p. 335) found that "the progress of the young larvae was very much accelerated when the leaf was moistened, and many died on a hot, dry day." In a condition where the relative humidity of the air is 50%, the larva, if it ever hatches, has great difficulty in making its way down the leaf. In every case under this humidity the larvae failed to move but short distances and invariably died. Too much water, e.g., rain, will also be detrimental for then the larvae are likely to be washed away from the plant. Excessive dew may produce the same result.

Influence of Light and Darkness.—Not enough work has been done to justify any statement concerning the behavior of larvae under various conditions of light, but judging from the result obtained in an artificial cave where the light is very weak, the general behavior of the larvae seemed not at all modified from that in the bright light.

DISCUSSION AND CONCLUSIONS

The most interesting thing that was found so far as this study has progressed concerning the behavior of the larva, is the fact of orientation immediately following hatching. Regularity of its occurrence is significant. Possible advantages to be derived from this arrangement are not difficult to see. Since the eggs are laid normally with their anterior end pointing away from the base of the leaf, and since the larvae emerge from that end of the egg, the larvae must, under ordinary circumstances, turn round before they could possibly get down into the leaf-sheath, a process absolutely necessary for the life of the larvae. The orientation is therefore a distinct advantage to the larvae for it helps the latter to find their way quickly and properly. Furthermore, by being set in the right direction, the larvae are so directed as to minimize the period of exposure to the adverse conditions, for it is obvious that the sooner the larvae get down into the leaf-sheath, the safer they will be from the possible dangers, such as mechanical injury, attack from parasites and predaceous enemies, desiccation, etc. It is beyond the scope of this paper to discuss the force that is responsible for this phenomenon of orientation. Whatever the nature of this directing force may be, the fact of orientation certainly is an adaptation, a process distinctly advantageous in the life economy of the insect. As to the nature of the stimulus or stimuli in response to which the larvae manifest the migratory behavior, experimental data are lacking, but from the nature of the case, this phenomenon of migration might be interpreted as the result of positive thigmotropism and also possibly of positive geotropism. It is interesting to note that Enock (1891) found that the larvae moved towards the tip of the leaf when the eggs were deposited in an inverted position but he failed to notice the orientation of the larvae on hatching. Gossard and Houser (1906, pp. 4-5) seemed to have had difficulty in making the larvae ascend a slope of about 45 degrees. In the present work, however, it was found that the larvae are not only able to ascend an inclined leaf (to the height of 139 mm., in one case) standing almost perpendicularly, but they do so regularly if the eggs are laid in an inverted position.

The reason quoted by Packard (1883, p. 212) why the red wheat is less injured by the fly than the white wheat needs revision, because the sloping leaf has nothing directly to do with the larvae working down " the wrong way." Whether the larvae are assisted by dew in their migration down the leaf blade, as suggested by Headlee and Parker (1913, pp. 95-96), needs, in the writer's opinion, closer scrutiny for the data on hand seem to indicate that the larvae find great difficulty in overcoming the surface tension of drops of water and, furthermore, dewdrops do not always roll to the base of the leaf-blade and stop there until the larvae are safely discharged.

SUMMARY

1. The direction of the migration of the larva in its initial stage is predetermined by the orientation of the eggs. The larvae on hatching always turn from the anterior toward the posterior end of the eggs.

2. The degree of inclination of the leaf has nothing to do with the direction of the larval migration.

3. The larvae are capable of locomotion on either an ascending or descending incline of anywhere between zero and 90 degrees.

4. When the eggs are laid with their anterior ends toward the base of the leaf, the larvae, on hatching, crawl up the leaf

until they reach the tip, then turn and move downward. The larvae may die while on this ascending migration but apparently never try to change the direction of progress.

5. The rate of migration is extremely variable and seems to be influenced by individual differences rather than physical factors. The average time required by 205 larva hatching from eggs laid normally to move one millimeter was about four and one-half minutes, with extremes of one-half minute and seventy-five minutes. The average time required by 119 larvae hatching from eggs deposited in an inverted position to move one millimeter was about three and one-half minutes, with extremes of two-fifths of a minute and forty-six minutes.

6. The mortality of migrating larvae is greatest when the eggs are laid in an inverted position. Twenty-three per cent of the larvae hatching from eggs laid normally died on migration, while fifty-seven per cent of the larvae hatching from eggs deposited in an inverted position perished.

7. When the eggs are deposited normally, the per cent of mortality increases with the distance of the egg from the ligule. When the eggs are laid in an inverted position, the mortality increases with the distance of the egg from the tip of the leaf.

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REACTIONS OF OPALINA RANARUM

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1. INTRODUCTION

Although the anatomy and reproduction of Opalina ranarum have been carefully studied, the reactions of this mouthless entozoic infusorian have not been so thoroughly investigated. Probably the most comprehensive recent work is that of Metcalf ('09) who gives a splendid chronological review of the literature. The first account, however, which deals with reactions, is that of Kühne ('59) who describes the effect of a strong induction current on Opalina. Several years later, Nussbaum ('86) briefly described the structure and the method of swimming in the introduction to his theme on reproduction. In 1888, Entz worked on light reactions and concluded that Opalina was negative to light. A year later, Verworn ('89) obtained results on the effect of light which were exactly opposite to those of Entz. Verworn treats also of reactions to heat stimuli.

Experiments in galvanotropism were performed by Birnkoff ('99), Pütter ('00), Kölsch ('02), Wallengren ('03), and Hartog ('06). Dale ('01) gives the most detailed account yet published of chemotaxis and describes very carefully the movement of cilia and their behavior to chemical and electrical stimuli. Veneziani ('04) experimented with culture media of varied chemical composition and showed the effect of each on Opalina. His work was continued by Pütter ('05) who discovered that a medium prepared from sodium chloride, sodium and potassium tartrate and distilled water was best. The work of Jennings ('06) concludes the list of publications on the behavior of Opalina.

Opalina is a large ovoid protozoan completely covered by a pellicle and therefore without mouth or anus.[1] It is strongly flattened dorsoventrally and somewhat asymmetrical at the more pointed anterior end of the "adult" animal, (Fig. 1). From the anterior end to the notch, in the middle of the right side, the surface of the body is concave, and below the notch, this side is markedly drawn in. The left side shows no such irregularity. Cilia are distributed abundantly over the entire pellicle; on the dorsal and ventral surfaces. They are arranged in diagonal rows across the body. Small Opalinas or those formed by recent divisions usually have the posterior end more pointed than the anterior.

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[1] Some of the earlier investigators (Künstler, '06, and Gineste, '06) claimed that a minute mouth was present on the ventral surface of the body, but their view has not been accepted by recent observers. The writer has made every effort to discover such an opening but without success. Specimens stained slightly with Delafield's haematoxylin and placed in a thin solution of gelatin afford excellent opportunity for observation but nothing could be discovered except little evanescent folds which frequently appear when the body is in the proper position.

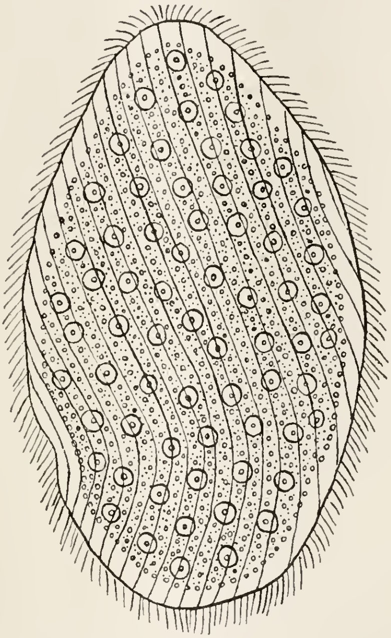

FIG. 1.—*Opalina ranarum.* Ventral view (after Dolflein)

The object of the present paper is to present a general account of the behavior of Opalina and to compare its reactions with those of free-living protozoans which are well known through the work of Jennings, Mast, and others.

The experiments discussed in this paper were performed in the Zoological Laboratories of the University of Wisconsin during the months of January, February, March and April, 1915. My thanks are due to Professor A. S. Pearse, under whose direction the work was done. Practically all material used was obtained from the rectum of leopard frogs, *Rana pipiens*, which were kept in a tank of running water in a vivarium. Although the room was heated, the temperature of the water ranged from 2° to 10°C.

Zeller ('76) observed that large Opalinas seemed to be absent from frogs in the month of January. This might be the case if frogs are allowed to remain in their natural habitats. During the present observations, however, Opalinas were apparently normal throughout the winter, though all frogs examined were not infected. Dobell ('07) pointed out that lack of food and increase in the number of bacteria in the rectum of the frog were causes of degeneracy in Opalina. In several instances, the writer noted that Opalinas were not found when there were no faeces or when the bacteria were few in number. The largest numbers were obtained when there was a considerable quantity of faeces and when the number of bacteria was comparatively large.

Material for observation was usually obtained from a frog by pithing or quickly chloroforming it. Pütter's saline medium, already mentioned, or a physiological salt solution made suitable culture media except when chemical stimuli were used. In the latter cases, it was found that by forcing water down the alimentary tract of the frog, a sufficient amount of liquid to serve as a medium for observations could be obtained without interfering with the normal activities of the Opalinas. When the medium was ready for use, enough was dropped on an ordinary slide to nearly cover one-half of it. If another liquid was introduced, it was carefully added with a dropper drawn to a fine point. Frequently the drop of chemical was placed next to the medium containing Opalinas, and then by the aid of a needle, was induced to flow across gradually. Experiments with colored liquids showed that diffusion took place quite slowly and that sometimes the introduced drop remained in only a small portion of the medium. A cover glass was usually not used.

OBSERVATIONS ON LOCOMOTION

Considering the environment of Opalina, it may be justly called a comparatively active creature, especially immediately after division. Other investigators have noted that the smaller individuals are extremely active and swim rapidly as if in a state of excitement. Unless stimulated, the mature Opalina moves very smoothly and bends its body gracefully as it wanders in and out among the debris. Finely ground India ink and gelatin were used successfully in observing the movements. Opalina was frequently found at rest either at the edge of a drop of culture medium or against a bit of the faeces. It keeps its cilia in active motion, however, at all times and apparently does not attach itself in the same way that Chilomonas, Didinium, and Paramoecium do.

The action system is essentially like that of many free swimming ciliates and flagellates. Opalina usually swims through the water in a spiral course, but quite often one is seen swimming without revolving on its long axis. Like many other ciliates, such as some Hypotricha and Colpidium, it often swims forward keeping one side against an object or in contact with the edge of a drop of liquid. In making its screw-like revolutions, Opalina turns over to the right. It was noted that Opalina does not make as many revolutions for a given distance as Paramoecium. Sometimes, it makes only half-revolutions at varying intervals, and then turns over toward the left for a time. There is another characteristic movement which does not seem to have been noted in other ciliates. Frequently, after making half a revolution, an Opalina will turn back the same distance, and repeat this movement several times in rapid succession.

The spiral course is much like that of Paramoecium as described by Jennings ('06). There are two factors which seem to influence this particular type of movement in Opalina—the forward movement of the animal, and the rotation on the long axis to the right. Cilia extending from the left to the concave edge on the right, beat directly backward and bring about the forward movement. The rotation on the long axis is due to the fact that the cilia on the surface of the body beat obliquely to the right and backwards. The revolving to the right is probably partly due to the asymmetrical form and partly to the cilia at the anterior end which beat obliquely forward. If all the cilia beat directly backward the animal moves forward without rotating. The cilia on the surface of the body beat in a rhythmic wave-like manner. Objects, caught in the cilia at the anterior end, were carried down the surface of the body in jerks. The cilia on a pair of conjugating Opalinas beat in harmony until the animals are ready to separate and then each set of cilia beats so as to part the pair.

AVOIDING REACTIONS

Opalina reacts to stimuli by using avoiding reactions similar to those of Paramoecium, Chilomonas (Jennings, '06) and Didinium (Mast, '09). It backs for a short distance without revolving on its long axis, and after turning to the right, swims forward at an angle to the original course. Sometimes the angle may be as much as 90.° An Opalina may make " tests " in several directions, moving forward or to the side, trying the conditions until they prove to be satisfactory. When reacting to some stimuli, Opalina swims in a circle without revolving and keeps the left side away from the center of the circle. Certain stimulating agents cause it to turn " somersaults " by bending up the anterior end and going over and over, but this type of reaction was not common.

In several instances it was possible to be very certain of the exact position of the body during rapid movements on account of a little blister or some other peculiarity. Individuals which came in contact with objects did not always back away but sometimes turned directly to the right. The locomotion of a conjugating pair is similar to that of single individuals.

REACTIONS TO MECHANICAL STIMULI

While swimming in a normal medium, Opalina frequently comes in contact with various objects and responds by the avoiding reaction already described. It may not retreat at all, however, but become fixed against a bit of faecal matter and remain in contact with it for some time; the behavior resembling Paramoecium against a bacterial zoögloea. If bits of filter paper are put into the medium, Opalina responds when it touches them with the avoiding reaction, or merely rests against them, beating its cilia as it does when standing against faecal debris. Occasionally, it moves along the edge, keeping the body close against the paper.

The ability to select food is not as evident in Opalina as in Didinium or Lacrymaria (Mast, '09, '11). Opalina does not readily discriminate between organic or inorganic matter for it will rest against a glass rod, a needle, or bit of filter paper, as readily as against faecal debris. Particles which might contain food are brought to the resting protozoan by the vigorous stroke of the cilia.

When the anterior end of Opalina is touched by a fine needle or a glass rod, the animal usually responds with the avoiding reaction. If the same stimulus is applied to the side of the body, there is usually no reaction, although there is occasionally a forward movement. Opalina will allow itself to be pushed along with a needle without attempting to move away.

REACTIONS TO CHEMICAL STIMULI

In studying the reactions of Opalina to chemical stimuli the fluid contents of the frog's rectum served as a medium in order to have conditions as normal as possible. This was usually alkaline, but sometimes slightly acid, and though such variations may have caused discrepancies they were probably neglible. Dale ('01) has carefully worked out the chemotaxis of Opalina in alkaline, acid, and neutral cultures. Opalina showed positive reactions to acids and negative to alkalies; but in an acid solution was negative to stronger acid and positive to alkali.

Although Opalina resembles Paramoecium in its responses to chemicals, it is usually slow in reacting to stimuli. It oftentimes swims quite a distance into a strong solution before reacting. The chemical, if injurious, proves fatal before the animal can make its escape. Usually, however, an Opalina will swim up to the border of a chemical solution and turn directly to the right. Like Paramoecium, Opalina sometimes enters and swims directly across a drop of a solution without response until it comes in contact with the original liquid on the other side, where it gives the avoiding reactions. As Dale ('01) pointed out, Opalinas are occasionally seen in clusters which are probably due to the presence of carbonic acid. The writer noted that Opalinas were frequently grouped together when taken from the rectum. As Mast ('12) noted in the case of Peranema, there was no evidence of orientation with regard to the direction of diffusion of the stimulus. Chemicals sometimes caused Opalina to swim in circles without revolving on the long axis.

When Opalina is dropped into distilled water, it swims hurriedly about for a time. Tap water placed next to a drop of culture medium was avoided for a short time, such water is less dense than the usual medium. Dilute salt solution induces the avoiding reaction when Opalinas are transferred to it from the rectum of a frog.

If an iodin-green or methyl-green crystal is dropped into a culture medium of Opalinas, they will respond by the avoiding reactions (Fig. 2). In some instances, they collected around the crystals but, as they are very susceptible to these chemicals, in a short time even comparatively dilute solutions caused death. Peranema (Mast, '12) is apparently much more resistant to the effect of iodin-green, methyl-green, and methyl-blue. Opalina avoids methyl-orange and a .4% solution of methylene blue (Fig. 2). If, by chance, it has ventured into these chemicals, it will turn to the right without revolving or backing, and find its way out. It was noted that some Opalinas which swam

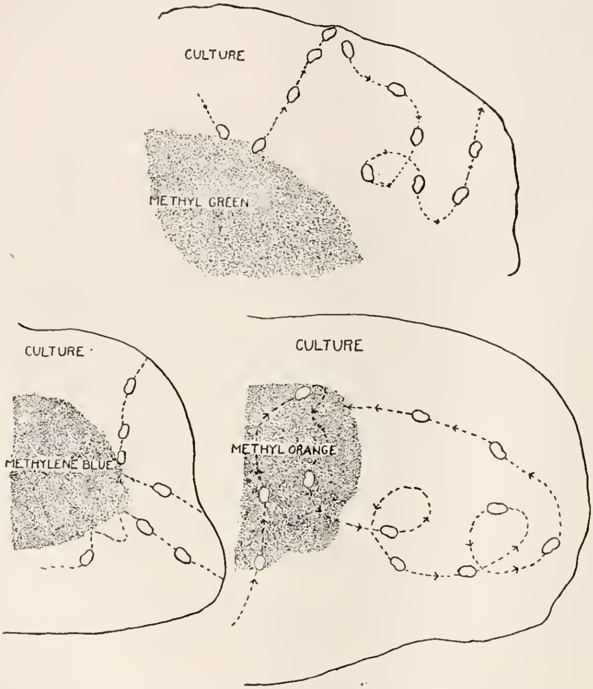

Fig. 2.—Showing reactions to chemicals

around in the chemical for some time would respond when encountering the culture medium.

Opalinas collected about acids introduced into the alkaline culture medium. Opalina is more susceptible to hydrochloric than to acetic acid. In one case, it was noted that Opalina lived in .01% solution of acetic acid for fifteen minutes before it proved fatal. Opalina reacts positively to nitric, sulphuric and formic acids. Even when acids were quite concentrated, it does not give avoiding reactions. The concentrations used varied from N–500 to N–10,000.

Opalina avoids neutral salts and those exhibiting basic properties. If a .2% solution of sodium chloride is added to the medium, Opalina, like Spirostomum (Jennings, '00) will avoid it by turning to the right and swimming off in a new direction. Opalina also responds by the avoiding reaction to a .005% solution of potassium hydroxide. It also is negative in its reactions to .02% to .002% solutions of each of the following salts: ammonium chloride, calcium chloride, potassium chloride, and a similar per cent solution of sodium hydroxide. In one case in which calcium chloride was used the strong repellent action was particularly noticeable; a large number of individuals, near the salt, moved away and crowded together at the opposite end of the slide.

TEMPERATURE

Unlike Paramoecium and Oxytricha, Opalina does not give the avoiding reactions to change in temperature. As Verworn ('89) observed, it swims indifferently from a warmer to a colder area and vice versa. If a quantity of culture medium, heated to about 40° C., is put on one end of the slide, Opalinas coming in contact with the warmer liquid swim actively about. When they approach the center of the heated area, motion ceases entirely, the cilia continue to vibrate rapidly for a few minutes, and then stop beating; the entire animal soon disintegrates. That Opalina is not very resistant to heat is shown by the fact that if it is allowed to remain in a temperature above 22° C., it dies in a short time. If Opalina is dropped into a heated medium, it does not respond by the avoiding reaction as has been observed in Pleuronema (Jennings, '06). Opalina shows a very great resistance to extremely low temperatures. It does not react to water at 2° C.

Temperature reactions were also studied by siphoning water of various temperatures through an exceedingly fine capillary U-shaped tube. With this apparatus a more uniform and definite temperature was obtained. The tube which rested on the slide was observed under a microscope. Opalina swims indifferently up to the cold or warm tube, rests along the surface or may move along in close contact with it.

REACTIONS TO LIGHT

Light induces no change in the movements of Opalina as is also true of Paramoecium and other colorless ciliates. Neither an increase in intensity nor a decrease causes a response. Contrary to what Entz ('88) observed, Opalina may be suddenly exposed to very bright sunlight and then quickly shaded without causing it to react. There was no evidence that it oriented in horizontal rays of light. In one instance, where a number were oriented in the direction of the source of light, there was no response when the slide was turned 180°. Polarized light or red light have no effect on movement.

In some of the experiments with light a Nernst lamp of about 650 candle power was used in a dark room. By moving the light to various distances, varying from 12-178 inches from the Opalinas, different intensities were obtained but no reaction was noted.

SUMMARY

1. Opalina usually swims in a spiral, though it frequently travels long distances without rotation, or moves along the surface of some object without turning over. When feeding it remains in contact with the debris and keeps the cilia vibrating rapidly.

2. The spiral course is due to the forward movement of the organism and the rotation on its long axis. Opalina often makes half a revolution and then turns back the same distance.

3. Opalina reacts to stimuli by moving backward a short distance without rotating and then turning to the right at an angle to the original course. If it is stimulated, it "tries" many different directions until one is found which proves satisfactory. When stimulated Opalina often swims in a circle, without revolving, keeping the left side turned away from the center.

4. Mechanical stimuli sometimes induce the avoiding reaction. Opalina frequently swims indifferently up to glass, needle, filter paper and other objects, remaining against them as if in contact with food. Opalina responds by retreating when the anterior end is touched with a fine rod but does not react when the side of the body is stimulated.

5. Opalina lives in both acid and alkaline media. When in an alkaline medium it reacts positively to acids and negatively when encountering neutral and basic salts. It may cease to react to a chemical after repeated stimulation and remain in the chemical. Solutions of different strengths cause the avoiding reaction when Opalina swims from one to the other. Opalina does not avoid strong acids.

6. Opalina does not react to heat or cold. It is much more resistant to cold than to heat. It may live at temperatures of from 2° C. to 22° C.

7. Light apparently has no effect on the orientation or movement of Opalina.

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SIMILAR BEHAVIOR IN COW AND MAN WITH A NOTE ON EMOTION

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The two incidents herein described present features of such similarity that they seem worthy of record among investigations bearing on comparative problems and especially among statements concerning instinctive (?) tendencies.

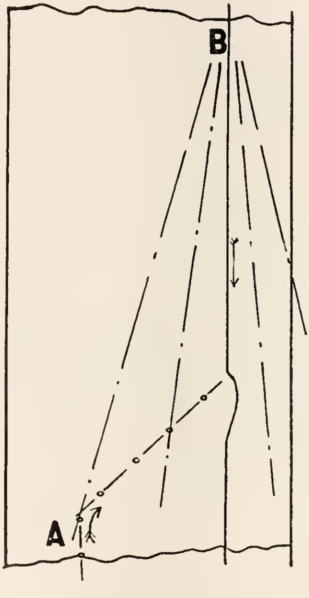

FIG. 1

Fig. 1 gives the essential features in the setting of the first incident. The Jersey cow was walking along the side of the road toward us, near the position marked A, when the light of the automobile at B, first disclosed her presence. As the car approached her, going in a straight line as indicated, she turned in an easy curve, not abruptly, and walked in the direction indicated. The distance across the road was relatively short, so that by the time the car reached her, the driver was forced to swerve the car sharply to our left to avoid hitting her head with the front fender of the car. As the front end of the car passed, the cow jerked her head sharply to the left and thus avoided collision with the rear end.

The incident occurred about seven o'clock in the evening. It was sufficiently dark so that objects to the human eye, when dark adapted, gave only indistinct outlines. In the lighted roadway in front of the car objects such as sticks, stones, and uneven places in the road-bed could be seen distinctly. At least four possibilities are open. The behavior of the cow may indicate some form of heliotropism, or the difference in distinctness of pathways may have operated to change the animal's behavior. A third hypothesis might combine the two factors suggested. We may also designate this behavior as habitual.

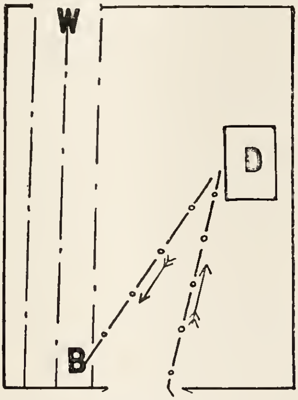

FIG. 2

Fig. 2 gives the surroundings of the second incident. My office is next door to the room outlined in the diagram. I was working by electric light one evening at my own desk and had occasion about eight o'clock to place some papers on the desk of this adjoining room. I entered the room, laid the papers on the desk, and returned to my own office. On my return, I found I had failed to replace all of the papers. Picking up those remaining, I retraced my steps. I placed the second set of papers with the first and started to return. On reaching the location indicated, B, my head jerked back and I turned abruptly to my left. I was not approaching the door as can be seen from the diagram.

For the first time, I now seemed aware of the setting of the situation in which I had just reacted as described. The moon's rays were shining through the window W, and lighted up an area of the wall and a few inches of the floor back of the spot marked B. The lighted area was about three feet wide and extended up two feet on the dark gray wall. In the corner of this illuminated area was a small, round gas stove and a few strands of insulated wire loosely coiled. The moon's rays did not reach the doorway by which I was attempting to pass out. The point reached, B, is approximately five feet from that one usually passed over in going out of the room by daylight.

Up to the point of the second change in pathway in order to avoid the wall and to go out by the door, the reactions of the cow and of myself are similar. Objectively the incidents may be described in identical terms and no one can seriously urge that consciousness took any prominent part in either subject's behavior. In the two cases, we have positive reactions whose settings are strikingly similar; and in the cow's head jerking to the left and in my own head jerking back, we can see the typical withdrawal reaction. Anecdotes are plentiful of horses and cows refusing to be driven from the lighted areas around burning barns, etc., but I can at present recall no case of so direct a human response to lighted areas, uncomplicated by implications of inner purpose.

The explanations suggested above for the cow's behavior appear accurate and complete here also.

After making the withdrawal reaction of the second trip, my consciousness of the situation included a distinct and clear revival experience accompanied by feelings of astonishment and excitement. My behavior now differed materially from the first form. I stopped, looked at the lighted area, turned around toward the window, and left the room slowly. No one who has made the two trips or had seen them made could avoid the conclusion that a distinct change in behavior had taken place. I now *knew* definitely that I had taken the wrong path on the *first* return trip also. (I fear the behaviorist will not read much further.) But the shift from the pathway toward the lighted area to that through the doorway the first time must have taken place quite smoothly for I can find no memorial evidence and no hints indicating perseverative tendencies in the recollections of the interval between the two trips. Nevertheless, after the second trip, I remembered the reaction of the first. Theoretically, the first reaction and the whole first trip must have persisted and modified the behavior on the second journey. For example, I could recall a slight, but noticeable increase in the speed of my movements as I placed the forgotten papers with the others,—placing these papers on my colleague's desk would close my work at the office for the evening. We may then postulate two new factors in the conditions of the second trip; on the evidence of recall, there was the perseverative influence of the first reaction; and there is distinct introspective evidence of a slight annoyance over the necessity of repeating the process.

Looking back over the few moments involved, I can find no form of evidence for believing that I was aware of going toward the lighted area. The instinctive or habitual behavior and the conscious processes seem ideally teased apart in the incident. The details of my thoughts were about the contents of the papers and my trip homeward; and I am unable to connect any portion of the mental process with the change in behavior that led away from the door on both return trips, and announced itself so vividly on the second. On the other hand, the mental processes connected with the behavior during the emotional excitement that followed the second reaction are clear. The kinaesthetic wave that localized itself in the muscles of the neck, shoulders, chest, and upper arms was distinctly noted at the time. Detailed thoughts about the lighted area, the relation of pathway to desk and door, astonishment at the sudden movements made, and a diffused intellectual excitement accompanied the later wavering behavior above described.

We cannot omit to recall in this connection, Professor Dewey's suggestions concerning a theory of emotions. Although the total equilibrium is not laid bare, nevertheless, the only ground for astonishment and excitement seems to rest in the sudden breaking of the steady progress toward the lighted area on the wall by the energetic jerk of the head backward. "What to do about it" is thrust forcibly into the foreground of consciousness. Briefly, we see that objectively the reactions of the cow and of the human are describable in the same terms. In the latter no preliminary conscious process is discovered to explain either the reaction to light or the withdrawal reaction. The conflict between the positive reaction to light and the avoidance reaction are the immediate precursors of a definite emotional state.

FREQUENCY AND RECENCY FACTORS IN MAZE LEARNING BY WHITE RATS

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Let us assume that the number of previous runs in any unit of the maze (frequency) determines the direction a rat running the maze in the process of learning will take at any bifurcation encountered, and that probability alone governs the early " choices " at such positions.[1] On these assumptions an interesting explanation of maze-learning by rats has been made. Let us start an imaginary rat in a ten-*cul-de-sac* maze and determine its course at each bifurcation by flipping a coin: " heads," it keeps its direction—forward or return, in whichever it happens at the time to be going; " tails," it enters the blind alley. On emergence from the blind alley, " heads " again takes it in the direction it had when the blind alley was encountered and " tails " means a return, the reverse of that direction.

The results of one such trial are here given to make more concrete the method. F in the lower line means movement toward the food box (forward) and R signifies a return, the reverse direction. An R *underscored* means that the return is complete and that the direction of movement is reversed, putting the animal again at the first bifurcation—at the first blind alley. The figures represent blind alleys entered.

h t h t h t t t h t h h h t h t t h t h h h
F 2 F 3 F 4 R 3 R 2 R *R* F 2 F 3 R R 1 *R* F F

h t t h t h h h t t t h t t h h h h t h t h
F 4 R R 2 R *R* F 2 R 1 *R* 1 *R* F F F F 5 F 6 F

t t t t h h h h
7 R 6 F F F F F (to food box).

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[1] Throughout this discussion the word "choice" is used in the sense of going into one of two possible alleys open to the animal at any given bifurcation in the maze, not as implying any voluntary selection.

Figure I, a schematic maze with ten blind alleys, will make the results clear as recorded. The reader should keep the rule in mind and follow the rat through in detail. It will then be clear why a returning animal emerging from a blind alley gets F for a *t* and a second F for an immediately succeeding *h*, and *vice versa*.

Numbering and lettering the sections of the maze as shown in the figure, we may tabulate the choices of our hypothetical rat at the several bifurcations in a convenient manner for close inspection (Table I). The data of the first trial, already given on the previous page, are here tabulated as " trial 1." The other trials were made in the manner already described. The four trials are sufficient to illustrate the point in mind, and the method of analysis to be applied to results of actual rats learning the maze. In the table the letters Fd and Rt in the second column, under the caption " direction," show whether the animal was running forward or whether it was returning when the scores in the line in question were made. Thus the record starts with the animal passing *cul de sac* 1 and entering 2. That is, the first choice is B, the section of the correct path, the next is the second blind alley; then the forward direction is taken on emergence from 2, and 3 is entered; again the forward direction, and 4 is entered. From this point the animal makes a complete return, entering 3 and 2, but not 1 on the way; and so on. The summary of results of the individual trials and the general summary of the four trials show separately, for each lettered section of the maze, the total runs for each direction—Fd and Rt. In the case of the blind alley sections these two sets of totals, for forward and return runs, are combined, since the animal traversed those units in the same direction whether the blind alley was entered on a forward or on a return movement.

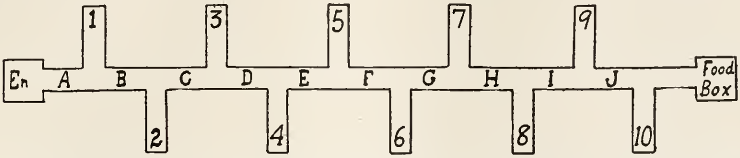

FIG. 1.—A schematic maze to show the lettering and numbering of the different sections. Numbers indicate blind alleys.

TABLE I

	Maze											Parts									
Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 1—Fd......			1	1	1	1	1	1													
Rt......	1		1	1	1	1	1														
Fd......			1	1	1	1															
Rt......	1	1	1		1																
Fd......			1		1		1	1													
Rt......	1		1	1	1		1														
Fd......			1	1																	
Rt......	1	1	1																		
Fd......		1																			
Rt......	1																				
Fd......			1		1		1		1	1	1	1	1	1							
Rt......												1	1								
Fd......													1		1		1		1	1	1
Totals...........	5	3	5 4	5	4 3	3	3 2	2	1	1	1	2	2 1	1	1	0	1	0	1	1	1
Trial 2—Fd......		1	1	1																	
Rt......	1		1																		
Fd......		1																			
Rt......	1																				
Fd......		1																			
Rt......	1																				
Fd......			1	1																	
Rt......	1		1																		
Fd......		1	1	1	1		1	1	1	1											
Rt......	1		1	1	1	1	1		1												
Fd......		1																			
Rt......	1																				
Fd......			1	1	1		1	1													
Rt......				1	1	1	1														
Fd......					1	1	1		1		1		1	1	1		1		1		1
Totals...........	6	5	4 3	6	3 2	3	3 2	2	2 1	1	1	0	1	1	1	0	1	0	1	0	1

MAZE — TABLE I—*Continued* — PARTS

Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 3—Fd.....		1	1		1		1	1													
Rt.....				1	1		1														
Fd.....					1	1	1	1	1	1											
Rt.....						1	1	1	1												
Fd.....							1		1	1											
Rt.....	1		1		1	1	1		1												
Fd.....		1	1	1																	
Rt.....	1	1	1																		
Fd.....		1	1		1	1															
Rt.....	1		1	1	1																
Fd.....		1	1		1		1	1	1	1	1		1	1							
Rt.....										1	1	1	1								
Fd.....											1	1									
Rt.....						1	1		1	1											
Fd.....							1		1		1	1									
Rt.....		1	1		1		1	1	1		1										
Fd.....			1		1		1	1	1		1		1		1		1		1	1	
Rt.....												1	1		1		1		1		
Fd.....													1		1		1	1			
Rt.....																1	1				
Fd.....																	1	1	1	1	
Rt.....																		1	1		
Fd.....																			1		1
Totals..........	3	6	**5** 4	3	**5** 4	5	**6** 5	6	**5** 4	5	**4** 3	4	**3** 2	1	**2** 1	1	**3** 2	3	**3** 2	2	**1**
Trial 4—Fd.....			1		1	1															
Rt.....	1	1	1		1																
Fd.....			1		1	1	1		1		1	1									
Rt.....						1	1		1		1										
Fd.....							1	1	1	1											
Rt.....		1	1		1		1	1	1												
Fd.....			1	1	1	1	1	1	1	1	1	1									
Rt.....						1	1		1		1										
Fd.....							1	1	1		1		1		1		1	1	1		1
Totals..........	**1**	2	**3** 2	1	**3** 2	5	**4** 3	4	**4** 3	2	**3** 2	2	**1** 0	0	**1** 0	0	**1** 0	1	**1** 0	0	**1**
Totals of 4 trials	15	16	**17** 13	15	**15** 11	16	**16** 12	14	**12** 8	9	**9** 5	8	**7** 3	3	**4** 0	1	**6** 2	4	**6** 2	2	**4**

The totals are very interesting and seem to throw some light on maze learning. As would be expected on laws of probability, the numbers at the entrance end of the maze are much larger than those at the food end, though the diminution in the size of the numbers as the food end of the maze is approached (the right side of the table) is not entirely regular. This general decrease in the numbers toward the food end of the maze is obviously due in the main to the fact, not usually pointed out in maze learning, that any animal entering the food box does not return. This is not due simply, if at all, to the *pleasure of eating*; it is due to the conditions of the experiment. An animal entering the food box is *prevented* from returning. There are consequently on our record no returns in the section of the maze leading from *cul de sac* 10 to the food box. Hence, moreover, only one-fourth of all runs reaching 10—whether the animal enters or goes beyond it—result in returns from this point. This is the expectation statistically and our results of the four " trials " of the hypothetical rat only approximate this expectation, —2 to 4. As we shall see, this is a point of much significance which seems to have been overlooked in studies on maze learning.

In these results, derived by the laws of chance, the totals for all forward movements in the lettered parts of the maze—the sections making up the true path—amount to 96. For ease of detection these numbers are in bold face in the totals column. The total entrances to blind alleys are 88; and there are in all 71 returns over the lettered sections of the maze. These numbers come close to probability expectations, as will be shown. A forward-direction approach to any blind alley gives a probability of 1/2 that the blind alley will be entered and 1/2 that the correct path will be kept. If the *cul de sac* is entered the animal will return to the true path, at which point the probability is again 1/2 that the forward direction will be taken and 1/2 that the return direction will be chosen. This makes a total probability of 3/4 ($= 1/2 + 1/2$ of $1/2$) that the animal will keep the general forward orientation whether or not the blind alley is entered, and of 1/4 that it will be turned back at the blind alley (*i.e.*, 1/2 of the blind alley entrances will result in returns).[2] In general, of x approaches to any blind alley in the forward direction $x/2$ entrances to the blind alley in question will be made; $x/4$ returns will be made from this point; and $3x/4$ cases of keeping the general forward direction will occur. But on any return trip past the same blind alley these probabilities are reversed; there is now in x such cases a probability of $x/2$ that the blind alley will be entered, of $x/4$ that the forward direction in the maze will be resumed, and of $3x/4$ that the return direction will be maintained. Adding these fractions to those for corresponding directions above, we get a probability of x for entrance to the blind alley, of x for the forward direction, and of x for returns. That is, for any equal number of forward runs in the maze and returns to the place of starting—with the forward and backward intermediary movements that according to chance would result—the probability of entrances to blind alleys, of return directions of movement from such points, and of forward directions of movement would be 1:1:1, respectively. *In such a case there could be no learning at all so far as frequency effects go.* But since every trial in the maze must end with a forward run reaching the food box, as well as begin with a forward run, these respective probabilities would become $x + 1/2$, $x + 1/4$, and $x + 3/4$. In our totals, then, the expectations would be $40\ (x + 1/2)$, $40\ (x + 1/4)$, and $40\ (x + 3/4)$; or $40x + 20$, $40x + 10$, and $40x + 30$. We actually got 88, 71, and 96, respectively, a very close approximation. The coefficients, 40 in each case, represent 4 trials *times* 10 blind alleys to pass in each trial.

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[2] For simplicity we assume that returns occur only at times of emergence by the animals from *cul de sacs*, an assumption which does not do great violence to the actual behavior of rats.

If $x_1, x_2, x_3, \ldots\ldots x_{10}$ represent, respectively, the number of times that an animal gets successfully past blind alley *1*, *2*, *3*, ... *10*, and if for simplification we posit a condition such that whenever at any point the animal begins a return movement on emergence from a blind alley, it must continue the return to the starting place whatever other blind alleys may be entered on the return run, then according to pure probability laws $x_1 > x_2 > x_3 > \ldots\ldots x_{10}$. Just how much greater in each case? Evidently, according to the foregoing, $x_2 = 3/4$ of x_1, $x_3 = 3/4$ of x_2, $x_4 = 3/4$ of x_3, ... $x_{10} = 3/4$ of x_9. But x_{10} equals the total number of trials[3] that the animal has made up to the point of consideration in the experiment, or the total number of times that it has reached the food box, since each trial has only one run past *cul de sac* 10. Hence, if

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[3] Trial is here used in the sense of a continuous effort ending only when the food box is entered.

$$\begin{aligned}
x_{10} &= n, \\
x_9 &= 4/3 \text{ of } n = 1.33n, \\
x_8 &= (4/3)^2 n = 1.78n, \\
x_7 &= (4/3)^3 n = 2.37n, \\
x_6 &= (4/3)^4 n = 3.16n, \\
x_5 &= (4/3)^5 n = 4.21n, \\
x_4 &= (4/3)^6 n = 5.62n, \\
x_3 &= (4/3)^7 n = 7.45n, \\
x_2 &= (4/3)^8 n = 9.97n, \text{ and} \\
x_1 &= (4/3)^9 n = 13.32n.
\end{aligned}$$

In general, in a maze with y blind alleys the number of times that the first would be passed in forward runs in n trials is $(4/3)^{y-1}$ *times* the number that the last would be passed, *i.e.*, $(4/3)^{y-1}n$.

Now, on the assumption above, it is evident that the number of entrances to the respective blind alleys will be to the number of times that they are passed in the forward direction as $(x_1 - 1/4) : x_1$, $(x_2 = 1/4) : x_2$. . . . . $(x_{10} - 1/4) : x_{10}$.[4] Substituting the values determined above for x_1, x_2, x_3, etc., we get the following ratios of blind alley entrances to forward runs past blind alleys in order from the first to the tenth:

$$\begin{array}{rcl}
13.07n & : & 13.32n, \\
9.72n & : & 9.97n, \\
7.20n & : & 7.45n, \\
5.37n & : & 5.62n, \\
3.96n & : & 4.21n, \\
2.91n & : & 3.16n, \\
2.22n & : & 2.37n, \\
1.53n & : & 1.78n, \\
1.06n & : & 1.33n, \\
n - 1/4 & : & n.
\end{array}$$

Now when n equals any small number, as 1, 2, or 3, it is evident that the number of times of passing successfully a blind alley over that of entering it (*i.e.*, the practice-effect according to the law of frequency) is proportionately greatest for the *cul de sac* nearest the food box, and that it steadily decreases in order back to the first *cul de sac*. This would mean, on the basis of pure frequency factors in learning, that in general the nearest blind alley to the food box would be eliminated first, the second next, and so on. Elimination of all entrances to the last *cul de sac*—that nearest the food box—would then convert the maze in question for the given rat into a nine-blind-alley maze, elimination of the ninth *cul de sac* would make practically an eight-blind-alley maze, and so on, till the maze habit became perfectly established.

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[4] Each is passed 3/4 of the number of times it is encountered, and is entered 1/2 of that number. Since each trial has one extra forward run it is evident that the course past the blind alley has an advantage of 3/4 — 1/2, or 1/4, run or practice over the course leading into the blind alley. This advantage is not relative, but absolute; for an equal number of forward and back runs past any *cul de sac* gives equal frequency, as we have seen, for the two directions.

This would explain perfectly, then, a backward elimination of *cul de sacs* without any suppositions of "retroactive association," or of stamping-in effects of pleasure from eating the food, the effects varying inversely with the nearness of the pleasure. Since, however, the rat is not obliged to continue each return run to the starting place, and often does not do this, the mathematics of the above calculation is indefinitely complicated. We could go ahead and determine the probability of such complete returns from the second, from the third, from the fourth, etc., blind alleys; but such calculations would add nothing of further advantage to the theory we are testing. It is very certain, moreover, that the animal very early in the learning process eliminates most of the return movements.[5] In general, the following statement will suffice, and it finds support not only in theoretical determinations but also in results obtained by flipping coins as shown in the four illustrative trials tabulated in Table I: The greatest number of entrances to blind alleys occur in the part of the maze first to be passed through. This is because every animal reaching the starting place on a return must reverse its direction, while the contrary is true at the other end of the maze. Rats entering the food box cannot return into the maze. If the maze is one having many blind alleys, however, the animals may make comparatively many entrances also to *cul de sacs* in about the middle of the maze, so far as mere probability is concerned, for the chances of complete returns from distant parts of the maze are small. Near the food end of the maze the entrances to *cul de sacs* are fewer in number because (1) the probability is small that the animals will get to this part of the trial without making returns, and (2) there are no returns from the extreme end of the maze due to the fact that the food box holds all rats that reach this end. *Every blind alley must be passed in the forward direction at least as many times as the one nearest the food box—usually most of them are passed many more times than it is,—while this last one is never passed in the return direction* and hence is never entered from that direction. The other several blind alleys are passed generally in an increasing number of times as their distance from the entrance place in the maze decreases. Exceptions to this statement will, of course, occur; for example, Table I shows only one entrance to *cul de sac* 8 and two to 10. The law is a statistical law, dealing with probabilities, and the results of sufficiently numerous cases should conform to it. The result of this general law is, then, that the act of running past the blind alleys becomes more practiced—is more frequently performed—than that of entering them, and, to an even greater degree, than that of returning; and that the proportion of this excess practice in following the true path is greatest nearest the food box.[6]

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[5] Peterson, Jos. The Effect of Length of Blind Alleys on Maze Learning: An Experiment on Twenty-four White Rats. *Behav. Mon.*, Ser. No. 15, 1917. 24 ff.

This explanation, then, suggested by Carr[7] and later by Watson,[8] but here for the first time worked out more fully and applied also to the regressive elimination of blind alleys, seems to explain admirably on the basis of frequency effects, taken in a general way, (1) why entrances to the blind alleys nearest to the food box should be eliminated first, and why, in general, all *cul de sacs* should be eliminated in the order of their distance from the food box; (2) why the number of entrances to the several blind alleys should increase in the same order.[9] The explanation would hold, of course, as would all the above reasoning, only on the condition that all other factors influencing the choices at the various bifurcations of the maze—such as the length of the *cul de sacs* and their general direction with relation to the true path—remained equal at the different points.

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[6] This agrees with actual results obtained as published in the monograph referred to in the previous note.

[7] Carr, H. A. *Psychol. Rev.*, 1914, **21**, 161 f.

[8] Watson, J. B. *Behavior*, 1914, Ch. 7.

[9] To be considered on subsequent pages.

Any differences in such matters, such as are found in all actual mazes, will not affect adversely the explanation as a general principle; they can only disturb the accuracy of our predictions based on it in any given case.

What, then, can be said of this theory, that pure probability-frequency factors explain the rat's learning in the maze? In the first place, there is an inconsistency in the explanations based on the theory, which on closer examination seems seriously to limit the validity of the theory; and, secondly, rats do not as a matter of fact learn the maze in agreement with the expectations of the theory.

Let us take up the first objection. Assume that a rat on the first trial enters *cul de sac* 1, emerges from it and continues forward in the right direction, that it passes 2 and enters 3. Let us suppose that on coming out of 3 it takes the return direction. Frequency, then, will favor its entering 1 again, if it continue past 2, which would be a matter of probability. On emergence from 1 again it should go forward and once more enter 3. Pure frequency (and also recency) effects would therefore lead us to expect the animal to continue running from 1 to 3, 3 to 1, etc., indefinitely. As a matter of fact other control factors develop to throw the animal out of this routine. These may be either changing external circumstances or they may be varying intra-organic factors. *These conditions, then, become the directive factors in the learning.* When the animal is thus thrown out of the trial conditioned by frequency, probability may again determine the course in the part of the maze beyond the third *cul de sac*, but here again frequency effects would serve only to fix another circular type of response. Frequency does not seem to operate toward the elimination of errors, but only to stereotype action.

It may be argued that the effect of frequency (and recency) is not strong enough thus to fix wrong acts in the beginning of the learning process. More scope might thus be left for the operation of mere probability laws to show themselves in the early trials of the animal. This, however, would be tantamount to saying that learning did not take place in the early trials. If frequency is the determiner of the learning, the rate of its operation does not alter the case. Such an assumption, moreover, is contrary to fact; learning effects are marked in the first and second trials. The only escape from this difficulty to the theory would seem to be an assumption that frequency factors are wholly *nil* up to a certain point, after a given number of trials and successful arrivals at the food box, and that they then begin suddenly, or gradually, to operate,—an incredible hypothesis. It is evident from a careful study of individual records that frequency effects show themselves from the beginning of the experience of the animal in the maze, and that other directive factors are operative in bringing about learning in even as simple a case as this.

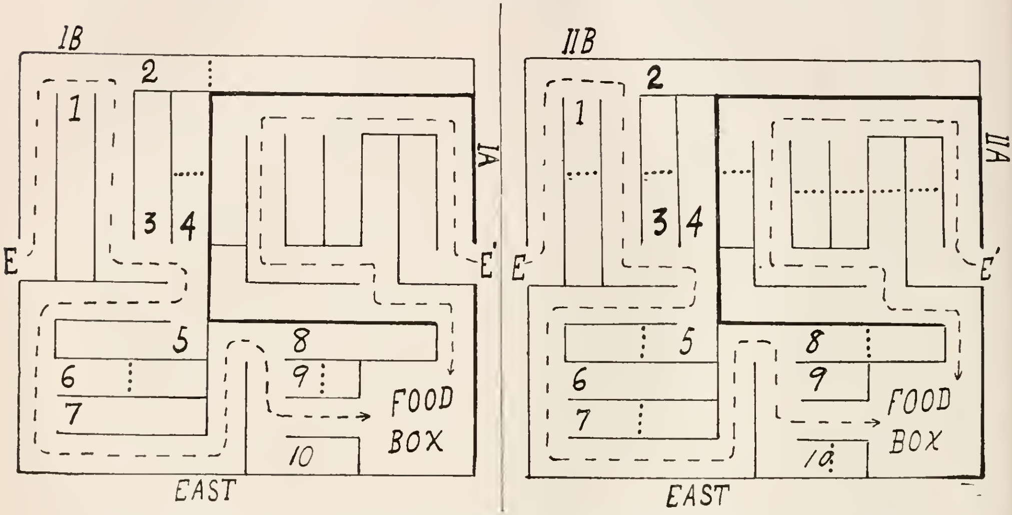

FIG. 2.—Mazes IB, IIB, and IA as used for present experiment. Dotted cross-lines mark the end of blind alleys in B-mazes. These mazes differ only in the relative lengths of blind alleys.

Our second objection is a question of fact. Do rats learn the maze in accordance with expectations based on frequency alone, or on frequency and recency? The question can be answered by a detailed examination of the actual records of several animals.

The method of tabulating individual records for detailed examination requires more space than can be expected for this article. A couple of samples of such tabulations up to points of nearly complete learning will be given, and results calculated from all the records at hand will be shown in more condensed form. The results are taken from experiments described elsewhere[10] on twenty-four white rats which were made to learn in different groupings two mazes of ten *cul de sacs* each and two of six each. For a description of the mazes, the procedure in the experiments, and of the animals the reader is referred to the other report. The results there given will be assumed to be familiar to the reader. In this connection we shall examine the records of seventeen of the rats in the mazes there described as IB and IIB (each with ten blind alleys), and IA (six blind alleys). Only the records of *un*trained animals, or animals without previous maze experience of any kind, will be considered. For convenience of reference the cuts of the mazes are here reproduced (Fig. II). Our present data are taken from animals running twice daily up to a point in the learning at which but few errors were made. The records of two animals in Maze IB and of one in Maze IIB were made useless for our present purpose by slight omissions in the record of the first day's trials.

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[10] Peterson, Jos. *Op. cit.*

Tables II and III show the several reactions of two rats tabulated in the manner explained in connection with Table I; the first is of an animal experiencing considerable difficulty (Rat 11), while the other is of one which much more quickly acquired the habit of keeping the correct path with but few errors (Rat 13). The records of the seventeen animals were all tabulated as those shown in the tables, except that the various " tallies " were first made with single lines. All records were then gone through carefully and the *critical choices* were marked in such ways as to indicate agreement or disagreement with expectations based on frequency and recency factors. Whenever an animal comes to a bifurcation in the maze that it has passed previously while going in the same direction, it is at what is called here a critical position, and its going into one of the rival alleys is a " critical choice." The second time that it arrives at *cul de sac* 1 on a forward run is an example. If it passed 1 the first time but now enters it, it goes *contrary* both to frequency and to recency expectations. The first return run in any section of the maze has critical positions only when the animal arrives at blind alleys which have been entered in the forward run. At such positions both frequency and recency factors favor entrance again, rather than a continuance of the return past this position in the true path. Entrance to such a *cul de sac* is *in accordance with* the expectations based on frequency and recency. There is no situation in which frequency factors operate alone with recency factors equally balanced, but there are situations in which the reverse is true. *E.g.*, suppose a given animal has entered *cul de sac* 2 (either in forward or in return runs, or both) twelve times, and also that it has passed 2 in the forward direction twelve times; the last of the two possible courses traversed is then the one favored by recency when 2 is approached by the animal going in the forwards direction. Frequency factors weigh equally for the two directions.

The following kinds of scores may be made by an animal at critical points: *Fr* = reactions favoring frequency but contrary to recency expectations; *Rf* = favoring recency, against frequency; *R* = favoring recency; *r* = against recency; *B* = favoring *both* recency and frequency; and *b* = contrary to both these factors. These symbols are used in the tables (II and III) here given to illustrate the treatment of the choices in the first three trials of each of the seventeen animals whose results are found in a condensed form on later pages. Choices scored " 1 " are uncritical choices.

In these tables only the first three trials are tabulated. The first trials are the important ones for the matter under consideration, in as much as the greatest changes in the behavior occur in the early part of the learning. The reason for this fact is obvious. In the early random stages of the learning any one of several single blunders is likely to throw the animal into confusion and bring about returns which lead to numerous other errors. It has been shown that the tendency to return is eliminated comparatively early in the process of learning the maze.[11] This fact is evidently responsible to a considerable extent for the very marked decrease in errors and time noticeable in the early trials. In the individual tables of the seventeen rats completed to the point of no errors in each record, it is found, as of course would be expected, that frequency-recency choices gradually increase in percentage, reaching at an early stage nearly 100%. Complete learning always gives 100% of such choices. *The meaning of this final preponderance of frequency-recency reactions is not that frequency and recency factors have brought about the learning*, but, more probably, *that some other factors have finally brought about the frequency-recency responses!*

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[11] See note 5.

TABLE II

MAZE RAT 11 MAZE IB PARTS

Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 1—Fd			1	1	1	1	1	1	1	1	1		1		1	1					
Rt				B	b	B	b	B	b	B	1		1		1						
Fd					B	B	r		b	B											
Rt	b	1	b		b	B	Rf		R												
Fd		R	r	r																	
Rt		B	b																		
Fd			B		b		b		R	B											
Rt								r	B												
Fd									B	B											
Rt		B	b	Fr	b		b	B	B												
Fd			B	B	r		Rf		r	B											
Rt			b	B	b	Rf	Rf		B												
Fd				B																	
Rt	b		R																		
Fd			B	B	(Tak	en ou	t of m	aze af	ter 40	min.	Sat	still i	n 2 a	long	time.)						
Trial 2—Fd			B	B	b		b	b	Fr	B											
Rt						Fr	b		B												
Fd							B	b													
Rt	Rf		r	BB	b		Rf														
Fd		b	Fr	B																	
Rt	b		B																		
Fd			B	B	b	r	Fr		r	B	b	b	r		B	BB					
Rt								r	b		r		B		B						
Fd									B		Rf		B	b							
Rt								B	Rf		B		R								
Fd									B	Fr	b	b									
Rt						B	b		b		R										
Fd							B		B	Fr	b		Fr		Fr	B					
Rt								Fr	b		B		B		B						
Fd									B	Fr	b		B		B	B					
Rt											B		B		B						
Fd											Rf	b	Rf		B		b	1	1	1	1
Trial 3—Fd		b																			
Rt	b																				
Fd			Fr	Fr	Rf	r	B	b													
Rt						B	b														
Fd							B		B	Fr											
Rt						B	Rf		Fr												
Fd							B	Rf	B	B	b		B		B	b	Rf	B	B		R
Totals	5	6	9 7	14	7 5	11	**11** 9	11	**13** 11	13	8 6	3	7 5	1	**6** 4	6	2 0	2	2 0	1	2

1 = uncritical choice; R = in accordance with recency; r = contrary to recency; Rf = in accordance with recency and contrary to frequency; Fr = the reverse of Rf; B = in accordance with both frequency and recency; b = contrary to both frequency and recency.

TABLE III

RAT 13, MAZE IB

			Maze													Parts					
Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 1—Fd......			1	1	1	1	1		1	1	1		1		1	1					
Rt......														1	1						
Fd......															B		b		1		1
Trial 2—Fd......		b	B	r	B		R		B	r											
Rt......						B	b	1	b												
Fd......							B		Fr	B	r		B		B		R	b	B	b	B
Trial 3—Fd......			B		R		B		B	Fr											
Rt......	b		b	B	b		R		b												
Fd......			B	R	Fr		B	b	Fr	B											
Rt......	R		b		b	Fr	r		R												
Fd......			B	r																	
Rt......	B		Rf																		
Fd......		b	Fr		b		Fr	b	Fr	B											
Rt......	Fr		Rf		Rf		r		B												
Fd......			B	r	B		B		B	B	b		B		B		B	b	B	Rf	B
Totals..............	4	2	7 4	6	6 3	3	7 4	3	7 4	7	3 0	0	3 0	1	4 1	1	3 0	2	3 0	2	3

Tables II and III show many evidences of effects of frequency and recency factors. For instance, Rat 11 (Table II) returned rather regularly in the first trial from *cul de sac* 5; in the second trial it went into 8 and returned from there three times—once entering 8 twice in immediate succession—and got its forward orientation again rather regularly at 4; in the third trial blind alley 3 became effective in turning the animal forward from returns. It will be noticed that in this trial the animal entered 4 on the forward run, due likely to the frequent entrances to 4 in the second trial, and that this led to a confusion and a return to 3.

It should not be overlooked, however, that some of these repetitive entrances to blind alleys may be due more to the position of these *cul de sacs* in the maze (*i.e.*, to the physical circumstances of the learning situation) than to frequency and recency. This seems particularly to be true of *cul de sac* 5 in the B-mazes and of 4 in Maze IA. The effect of such physical conditions is obviously to increase considerably in the early trials the apparent effects of frequency and recency factors as these are determined in the present paper. Making allowance for such matters, we find that the *influence for learning* of frequency and recency in the early trials is surprisingly small. In many cases, as has been pointed out, the influence of these factors is *against* learning, other factors having to throw the responses out of frequency channels. These other factors are in all probability *visceral*; *they are larger bodily reactions away from monotonous repetitions which are unprofitable to the entire organism.* Of late these factors seem to have been neglected in psychology under the dominance of the too mechanistic associationism. Physiologists in work like that of Professor Cannon on emotional responses are reminding us that the organism after all reacts in a unitary way according to its own organic needs. It would seem that while pleasantness and unpleasantness are likely not in themselves causal factors in behavior[12] these affective "states" are plainly indicative of visceral participation—probably inhibitions and facilitations which we have yet to discover—in the learning process.

A detailed study of the seventeen individual records is interesting from several standpoints. It shows not only the dangers of generalizations based on averages, on time and "error" curves without detailed analyses, etc., but also many marked individualities of the several animals. Since it is impossible to say how much mere probability has operated in these early reactions to critical positions in the maze, these reactions are less certainly significant of individual differences than are differences in the more general behavior—speed, cautious attitudes, etc.—so frequently commented upon by various writers.

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[12] Peterson, Jos. Completeness of Response as an Explanation Principle in Learning. *Psychol. Rev.*, 1916, **23**, 153-162.

Summarizing in tabular form the results of all the *critical* choices of the several animals of the three groups, and, finally, of all together, we get the following tables (Tables IV-XIV):

TABLE IV

Summary of Critical Choices of First Three Trials by Six Rats in Maze IB

	Trial number	r[13]	b	Rf	Fr	R	B	Totals
Rat 13	1	0	1	0	0	0	1	2
	2	3	5	0	1	2	10	21
	3	4	12	3	8	5	21	53
Totals		7	18	3	9	7	32	76
Rat 18	1	5	13	0	1	2	16	37
	2	3	4	2	0	1	6	16
	3	4	7	2	5	0	11	29
Totals		12	24	4	6	3	33	82
Rat 12	1	3	5	0	0	1	2	11
	2	8	8	0	3	0	10	29
	3	0	2	0	1	2	8	13
Totals		11	15	0	4	3	20	53
Rat 10	1	4	6	1	0	6	6	23
	2	2	13	3	8	5	16	47
	3	1	2	1	1	1	8	14
Totals		7	21	5	9	12	30	84

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[13] r = contrary to recency expectations; b = contrary to *both* recency and frequency expectations; Rf = in agreement with recency, and contrary to frequency expectations; Fr = the reverse of Rf; R = in agreement with recency expectations; B = in agreement with *both* frequency and recency.

TABLE IV—*Continued*

	Trial number	r	b	Rf	Fr	R	B	Totals
Rat 9	1	1	2	0	0	0	3	6
	2	0	0	2	1	1	7	11
	3	3	28	6	12	6	46	101
Totals		4	30	8	13	7	56	118
Rat 11	1	6	16	4	1	4	25	56
	2	6	21	6	10	2	36	81
	3	1	6	4	4	1	12	28
Totals		3	43	14	15	7	73	165
Grand totals		54	151	34	56	39	244	578

TABLE V

General Summary of the Six Rats in Maze IB

Trial No.	r	b	Rf	Fr	R	B	Totals
1	19	43	5	2	13	53	135
2	22	51	13	23	11	85	205
3	13	57	16	31	15	106	238
Totals	54	151	34	56	39	244	578

TABLE VI

Table V Expressed in Percentage

Trial No.	r	b	Rf	Fr	R	B	Totals
1	13.3	31.8	3.7	1.5	9.6	39.2	100
2	10.7	24.8	6.3	11.2	5.4	41.5	100
3	5.5	24.0	6.7	13.0	6.3	44.5	100
Totals	9.3	26.1	5.9	9.7	6.7	42.2	100
	$r + b = 35.4$			$R + B = 48.9$			

TABLE VII

Summary of Critical Choices of First Three Trials by Four Rats in Maze IA

	Trial number	r	b	Rf	Fr	R	B	Totals
Rat 7	1	5	3	0	0	2	1	11
	2	2	2	0	0	2	3	9
	3	3	6	0	0	1	5	15
Totals		10	11	0	0	5	9	35
Rat 5	1	0	1	0	0	1	0	2
	2	5	21	6	8	3	33	76
	3	0	7	0	2	0	14	23
Totals		5	29	6	10	4	47	101
Rat 1	1	5	3	0	0	0	1	9
	2	2	5	0	3	1	13	24
	3	0	0	2	0	2	3	7
Totals		7	8	2	3	3	17	40
Rat 8	1	1	2	0	0	0	3	6
	2	3	9	2	1	4	7	26
	3	2	0	1	0	0	3	6
Totals		6	11	3	1	4	13	38
Grand totals		28	59	11	14	16	86	214

TABLE VIII

General Summary of Four Rats in Maze IA

Trial No.	r	b	Rf	Fr	R	B	Totals
1	11	9	0	0	3	5	28
2	12	37	8	12	10	56	135
3	5	13	3	2	3	25	51
Totals	28	59	11	14	16	86	214

TABLE IX

Table VIII Expressed in Percentage

Trial No.	r	b	Rf	Fr	R	B	Totals
1	39.3	32.1	0.0	0.0	10.7	17.9	100
2	8.9	27.4	5.9	8.9	7.3	41.5	100
3	9.8	25.5	5.9	3.9	5.9	49.0	100
Totals	13.1	27.6	5.1	6.5	7.5	40.2	100
	$r + b = 40.7$			$R + B = 47.7$			

TABLE X

Summary of Critical Choices of First Three Trials, Seven Rats in Maze IIB

	Trial number	r	b	Rf	Fr	R	B	Totals
Rat 15	1	7	17	3	5	2	11	45
	2	1	1	1	1	0	9	13
	3	1	4	1	1	0	8	15
Totals		9	22	5	7	2	28	73
Rat 24	1	2	12	1	2	3	10	30
	2	2	8	0	3	3	10	26
	3	0	3	1	0	1	8	13
Totals		4	23	2	5	7	28	69
Rat 20	1	6	5	0	0	1	4	16
	2	2	1	1	0	2	7	13
	3	3	6	0	0	0	11	20
Totals		11	12	1	0	3	22	49
Rat 21	1	1	7	0	0	2	12	22
	2	2	8	3	5	2	17	37
	3	1	1	1	2	1	8	14
Totals		4	16	1	7	5	37	73
Rat 22	1	3	9	0	1	1	5	19
	2	4	4	1	4	3	7	23
	3	2	3	1	0	2	7	15
Totals		9	16	2	5	6	19	57
Rat 23	1	0	0	0	0	0	0	0
	2	4	20	0	1	3	17	45
	3	1	2	1	0	1	8	13
Totals		5	22	1	1	4	25	58
Rat 17	1	1	4	0	0	1	2	8
	2	4	16	2	0	3	14	39
	3	0	3	1	0	1	9	14
Totals		5	23	3	0	5	25	61
Grand totals		47	134	18	25	32	184	440

TABLE XI

General Summary of Seven Rats in Maze IIB

Trial No.	r	b	Rf	Fr	R	B	Totals
1	20	54	4	8	10	44	140
2	19	58	8	14	16	81	196
3	8	22	6	3	6	57	104
Totals	47	134	18	25	32	184	440

TABLE XII

Table XI Expressed in Percentage

Trial No.	r	b	Rf	Fr	R	B	Totals
1	14.3	38.6	2.9	5.7	7.1	31.4	100
2	9.7	29.6	4.1	7.2	8.2	41.3	100
3	7.7	21.2	5.8	2.9	5.8	56.7	100
Totals	10.7	30.4	4.1	5.7	7.3	41.8	100
	r + b = 41.1			R + B = 49.1			

TABLE XIII

General Summary of All Seventeen Rats in the Three Mazes

Trial No.	r	b	Rf	Fr	R	B	Totals
1	50	106	9	10	26	102	303
2	53	146	29	49	37	222	536
3	26	92	25	36	24	190	393
Totals	129	344	63	95	87	514	1232

TABLE XIV

General Summary of All Seventeen Rats Expressed in Percentage

Trial No.	r	b	Rf	Fr	R	B	Totals
1	16.5	34.9	2.9	3.3	8.6	33.7	100
2	9.9	27.2	5.4	9.1	6.9	41.4	100
3	6.6	23.4	6.3	9.2	6.1	48.3	100
Totals	10.5	27.9	5.1	7.7	7.1	41.7	100
	r + b = 38.4			R + B = 48.8			

It will be noted that the summaries of the first three trials of the animals of each group approximate rather closely the results of all seventeen, so far as combined recency and frequency relations are concerned; *i.e.*, 38.4% *against* the expectations based on recency alone and on both recency and frequency, and 48.8% in *agreement with* the expectations on recency alone and on both recency and frequency. The differences of physical conditions in the three mazes used—slight in the case of the B-mazes, differences only in the relative lengths of the *cul de sacs* similarly located with respect to the correct path—do not show themselves much in these results. Of course, only a small number of animals were tried on each maze and the present results need corroboration by more extensive studies. It is obvious that there is a gradual increase with successive trials, in all three mazes, in the reactions agreeing with recency expectations or with recency and frequency expectations combined; and that there is a corresponding decrease in reactions violating such expectations. Table XV shows this tendency. It would seem from this table that the change is most rapid in the easiest maze, IA, as is to be expected. It cannot be too strongly pointed out, as has already been mentioned, that this increasing percentage of reactions agreeing with the expectations based on recency and frequency effects, as learning advances from the first random stages toward the establishment of a regular habit, cannot be safely regarded as evidence that learning is brought about by recency and frequency factors: our evidence seems to justify the contrary conclusion, that this increase in reactions

TABLE XV

SHOWING GRADUAL INCREASE WITH SUCCESSIVE TRIALS IN REACTIONS FAVORING RECENCY AND FREQUENCY EXPECTATIONS

Trial No.	Four Rats in Maze IA		Six Rats in Maze IB		Seven Rats in Maze IIB		All Seventeen Rats	
	r + b	R + B	r + b	R + B	r + b	R + B	r + b	R + B
1	71.4	28.6	45.1	48.8	52.9	38.5	51.4	42.3
2	36.3	48.8	35.5	46.9	39.3	49.5	37.1	48.3
3	35.3	54.9	29.5	50.8	28.9	62.5	30.0	54.4

favoring recency and frequency factors is the *result* of the learning. A completed habit must give 100% of such reactions.[14]

It is not contended here that our results show the effects of frequency and recency on behavior to be negligible. On the contrary, their effects are obvious in any detailed study of the rat's learning in the maze, pursued by the method of analysis here developed. But so far as the bringing about of the short cuts (the elimination of useless acts) in learning is concerned, recency and frequency factors do certainly not seem to play the important part that they have been considered to play in maze learning. It is but natural to suspect that the same thing will hold for other types of learning. It seems that we are in need of searching analyses of the detailed aspects of all sorts of learning. Our initial spurt of progress in the study of learning has passed and mere time, error, discrimination, and average attainment curves of general results can no longer solve the problems that we are coming to as soon as we begin more detailed studies.

So far as experimental evidence goes at present it would seem that maze learning by rats agrees in the main with the results to be expected on the basis of probability-frequency factors as their general results were pointed out in the early part of this paper; that is, that the blind alleys nearest the food box are first eliminated, and that entrances to blind alleys are greatest near the starting place in the maze and decrease for the successive *cul de sacs* directly with their nearness to the food box. Recent results published by Hubbert and Lashley[15] seem to agree with this conclusion, though these results raise other problems the solution of which is not yet made clear. Miss Hubbert found in an earlier research[16] no invariable sequence in the elimination of blind alleys, but the more recent article cited admits that "when averages of very large groups of animals are taken there does seem to be progressive elimination of errors for the food compartment to the entrance of the maze."[17] Miss Vincent's[18] and my own[19] results show in general the same progressive elimination of errors.

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[14] See an erroneous conclusion by Hamilton in his interesting monograph, A Study of Perseverance Reactions in Primates and Rodents. *Behav. Mon.*, Ser. No. 13, 1916, pp. 38-46.

[15] Hubbert, H. B., and Lashley, K. S. Retroactive Association and the Elimination of Errors in the Maze. *Jour. Animal Behav.*, 1917, **7**, 130-138.

[16] Elimination of Errors in the Maze. *Ibid.*, 1915, **5**, 66-72.

[17] These averages as given in the later article are, going in the order from entrance place toward the food box: 30.6, 26.4, 19.7, 19.7, 18.7, 8.3.

[18] Vincent, Stella B. The White Rat and the Maze Problem. IV. The Number and Distribution of Errors: A Comparative Study. *Jour Animal. Behav.*, 1915, **5**, 367-374.

Hubbert and Lashley classified the errors in the circular maze into those of wrongly passing a door (type I) and those of turning in the wrong direction (type II). The errors of type I they found to be eliminated in less than two-thirds the trials necessary for the elimination of those of type II. The serial backward elimination of errors of type I was found to agree in the main with results of the other studies cited in the preceding paragraph, but no such serial elimination of the type II errors took place. They find, in accord with our own results, that the animals seem to orient themselves to the maze as a whole, favoring in the several blind alleys the inward direction which in the circular maze is always toward the food box. If the individual reactions of each animal had been studied more in detail these experimenters would likely have found the explanation of the differences in the method of elimination of the two types of errors. Our results, in the monograph already referred to, show that the animal soon learns to keep its general forward orientation in the maze, and also that the final stages of the elimination of blind alleys are frequently accompanied by a confusion to the animal which results in entrances to *cul de sacs* nearer the food box, already eliminated. A study of the situation in the circular maze seems to suggest that the early development of the forward orientation tendency would tend to throw the animal into the blind alleys entrance to which constitutes errors of the second type. In every case a rat keeping its general forward direction and avoiding the error of type I would be thrown into an error of type II. This condition certainly would seem to invalidate the authors' general conclusion as to the relative frequencies of elimination of the two types of error. Moreover, since the rate of elimination is studied in terms of the number of trials required to avoid successfully the entrance to a blind alley, it must be recalled that the final trials for elimination of the *cul de sacs* first encountered will bring about confusions resulting in entrances to some of those already eliminated, further along the trail. From these confusions errors of type II would most probably result, for the reason already indicated. The matter seems to need further investigation. These difficulties make plain how necessary it is to avoid the fallacy of assuming—and these authors, I believe, do not assume this—that each response can be considered on its own account, rather than in relation to other reactions concerning vitally the welfare of the entire organism. It would seem that with a different arrangement of the relations of the two types of blind alleys in the circular maze, so that the objection here urged would be met, results in this maze would in general agree with those obtained in the use of other mazes,[20] showing that on the whole there is a progressive backward elimination of errors in the maze. There are, of course, many circumstances, making entrances to certain *cul de sacs* more probable than to others, that tend against this general rule. No maze in existence has *cul de sacs* all presenting equal difficulty to the animal.

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[19] Cited in note 5.

The writer believes that in spite of the shortcomings of the frequency factors as an explanation principle of maze learning, the general considerations which he has discussed in the first (the theoretical) part of this paper satisfactorily account for the progressive backward elimination of errors in the maze, to the extent that it actually occurs, and also for the fact that the number of entrances to blind alleys increases roughly with their distance from the food box. There seems to be no "retroactive association" necessary, as Hubbert and Lashley rightly conclude.

If frequency and recency factors play the unimportant part in actual *learning* that our present data seem to indicate, to what neural and physical conditions, then, must we look for the main factors that bring about the elimination of random acts and the *changes in behavior* characteristic of learning? The writer has attempted elsewhere to indicate in a general and tentative way the answer to this question. In support of his contention that our neural explanations have usually been so simple as to throw us into a mechanical associationism which finds difficulty in explaining the changes in behavior characteristic of learning; that neural processes are inconceivably complex so that the general consistency of the circumstances, organic and extra-organic, forces short-circuiting of impulses in the central nervous system,—in support of this position the writer is pleased to quote a few lines from Professor C. J. Herrick[21] which have come to his attention since the former articles were written:

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[20] Cf. Carr, H. A. Distribution and Elimination of Errors. (An abstract.) *Psychol. Bull.*, 1917, **14**, p. 58.

[21] *Introduction to Neurology*, 1916, p. 306. See also page 296 and Ch. XXI.

"Between the sensory projection centers and the motor areas are interpolated the association centers, and these are so arranged that all correlation, integration, and assimilation of present sensory impulses with memory vestiges of past reactions are completed, and the nature of the response to be made is determined before the resultant nervous impulses are discharged into the motor centers. Only such of the motor areas will be excited to function as are necessary for evoking the particular reaction which is the appropriate (that is, adaptive) response to the total situation in which the body finds itself. This arrangement of association centers in relation to a series of distinct motor areas provides the flexibility necessary for complex delayed reactions whose character is not predetermined by the nature of the congenital pattern of the nervous connections."

Through our inheritance from association psychology we seem to have fallen into a narrow, mechanical view which in the case of our own conduct belies our introspective reports, a view which is narrow and untrue not because it attempts to be biological as opposed to spiritualistic but because it so much neglects the larger visceral reactions with which we are just now becoming better acquainted. The reaction away from monotonous and unprofitable repetitions, of which we have found so plentiful illustrations in the rat's maze-learning, is similar to what we find in our own conduct. Professor Dodge, in his presidential address before the American Psychological Association, emphasizes a view in his treatment of the subject of fatigue which seems to agree with our own. On the particular point in question, the influence of general visceral demands, he says: "In my own case I have been interested in observing how every prolonged period of monotonous work like correcting papers, for example, finds before its close some insistent demand for interruption. If I successfully suppress one demand, more insistent ones arise, until finally effective voluntary reinforcement of the main task suddenly ends."[22]

SUMMARY AND CONCLUSION

Working on Professor Watson's suggestion, that probability determines the early reactions of the rat in the maze and that the principle of frequency finally determines which of the various random acts will survive, *i.e.*, that it brings about the learning, we have found by flipping coins that probability does afford an explanation of how the animal finally reaches the food box in the maze, but that it fails to explain alone or in connection with recency how the useless acts are eliminated. Recency and frequency factors do not seem to explain how the short-cuts in behavior characteristic of learning come about. Probability and the effects of recency and frequency factors supplemented by certain visceral directive factors, do, however, seem to account in a satisfactory manner both for the elimination of *cul de sacs* in a progressive backward order, roughly speaking, and also for the greater number of entrances to *cul de sacs* in the first part of the trail and for the general correlation between the number of such entrances and the distances of the respective *cul de sacs* from the food box.

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[22] Dodge Raymond. The Laws of Relative Fatigue. *Psychol. Rev.*, 1917, 24, 89-113. Quotation is from page 111.

Tabulations of the reactions of seventeen rats in their first three trials in three different mazes—six in one, four in another, and seven in the third—show that, contrary to certain current views, over 50% of the rat's early critical choices at bifurcations in the maze are the opposite of what would be expected on the basis of recency and frequency factors. Responses favoring expectations on recency and frequency increase and finally reach 100% when the learning is complete. This, however, is not evidence that these factors bring about the learning. The converse is true: the modification called learning increases frequency and recency responses. It is suggested that this may also be true of other types of learning.

There seems to be clear evidence of the operation in learning of visceral factors controlling, for the general demands of the organism, the associations which are formed. Choices at bifurcations in the maze are not predictable on the basis of frequency and recency alone as applied to individual responses; each response must be considered in the light of the whole situation to which the animal as a unitary organism is reacting. The elimination of random acts, of entrances to *cul de sacs*, seem to be comprehensible only on this basis. This seems to indicate that the laws of association are not the dominantly controlling factors that they have credit for being in current psychology.

An analytic method of studying learning in the maze is developed, one which may be applied to other simple types of learning when the necessary controls are available.

THE ALTERNATION PROBLEM

A Preliminary Study

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INTRODUCTION

In the discrimination experiment animals are required to choose between several paths according to some given temporal scheme. It is recognized that the animals may ignore the stimuli to be discriminated and solve the problem by reacting to this temporal order of presentation. This possibility is usually eliminated by several means:—1. By instituting a sequence of such complexity that the animals are unable to master it. 2. By varying the given temporal order after the problem is mastered; and 3, by removing the stimuli and requiring the animals to rely upon sequence alone. The control tests have almost invariably shown that the sequence factor is relatively insignificant in the solution of these problems.

The ability of animals to master given sequences of position habits has not been adequately investigated. Such a problem presents several aspects of interest:—1. The determination of the limits of complexity which a given animal can master. 2. The relative difficulty of sequences differing in kind and degree of complexity. 3. The possibility of discovering new aspects of the learning process. 4. The determination of the various conditions conducive to the development of such habits; and 5, the character of the sensori-motor mechanisms involved in such series of alternating habits.

This paper reports the results of an experiment which was designed as a preliminary attack upon the above program. Before designing and constructing an apparatus especially adapted for this purpose, it was deemed advisable to test a group of animals upon a simple sequence. For this purpose we utilized a piece of apparatus which had been employed in the study of a particular phase of the discrimination problem. The essential features of this discrimination box are represented in fig. 1. The center consists of a 2′ x 3′ rectangular area. Opening from this enclosure are two exits, R and L, each 4″ x 4″ in dimensions. These exits are separated from each other by a distance of 6″, and they open into two runways, A and B, both of which lead to the food box F. These paths to the food box can be closed by means of two sliding doors situated at C and D.

A group of eight white rats was tested upon a simple alternation between two positions habits. On each trial the animal was taken from the food box and placed by hand at the position marked by an arrow in the figure. Both position and body orientation were kept constant from trial to trial, the head of the animal being placed at the position of the arrow head equidistant from the two exits. On the first trial of each day the path leading from the exit R was left open, while the path from L was blocked. On the next trial L was opened and R blocked, and this procedure was repeated for each day so that the order of presentation may be represented by the schema of R-L-R-L-R-L, etc. The number of trials per day was varied from two to eighteen according to the condition of the animal and the stage of learning. Progress in mastery was measured in terms of the percentage of correct choices, and a choice was termed correct whenever the proper door was entered sufficiently to secure a body orientation along the length of the passage

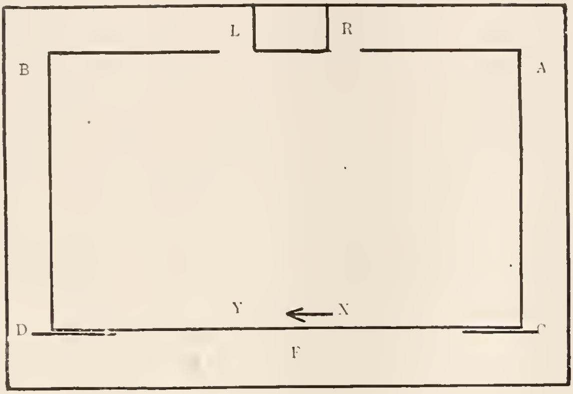

FIGURE 1.—Plan of apparatus. R and L, two exits; A and B, two pathways; C and D, sliding doors; F, food; Arrow, position in which rats are placed in apparatus; X and Y, two positions at which rats were placed in control tests.

way. The time devoted to a single run varied somewhat with the animal and the stage of mastery, but it became practically a constant after the first fifty trials. This time was determined for each animal for different stages of mastery. The average time per rat ranged from 21.5 to 25.5 seconds with a group average of 23. Of this time, 6.5 seconds were devoted to the run and 16.5 seconds to feeding and handling between runs.

ANALYSIS OF THE LEARNING PROCESS

All members of the group were able to master this simple alternation with a high degree of accuracy. A consistent record of 85% of correct choices for the group was obtained at the end of 600 trials. The number of trials per rat necessary to secure such a degree of proficiency ranged from 168 to 588, with a group average of 412. The number of trials for five of the eight animals closely approximated 450.

Three graphs representing progress in mastery are given in fig 2. The group curve is represented by the solid line. In its general features it is similar to the usual learning curve. The distribution of choices between the two exits is at first a matter of chance as the initial record is 50% of correct choices. The initial trials are more effective than the later ones though the curve approximates a straight line more closely than does the typical learning curve. There is some indication of the existence of a plateau beginning at the 340th trial. This phenomenon is to some extent a group artefact, though four of the eight individual curves give some indication of a plateau in this region. The individual curves exhibit some pronounced differences. Four graphs exhibit a relatively rapid initial ascent followed by a period of slower progress. Only one of these, however, approximates the typical learning curve. The curves for three animals exhibit an approximately straight line ascent; progress is uniform for all stages of mastery. One curve is quite unusual in this respect as it descends rather rapidly for 200 trials, then rises abruptly, and this period of ascent is followed by the usual slow progress. This curve is represented by the broken line graph of fig. 2. The dotted line curve represents the case in which the initial trials are relatively the most effective. These two individual curves represent the two extremes between which are to be found all degrees of gradation.

The animals were required in the initial trial of each day to choose the right exit in order to secure food. Alternation was the rule for the remaining trials of that day's test. Mastery of these initial trials thus represents a different type of problem from that involved in the subsequent alternation. For this reason separate records were kept of these initial trials and the results were plotted and the curve compared with that representing the mastery of the problem as a whole. 1. Mastery of this initial choice proved to be extremely difficult for the majority of the animals. Five rats consistently made poorer records for the first trial than for the whole day for all stages of learning. Only one rat found the initial choice to be easy and reversed the above relation. 2. Seven of the eight animals made poorer records for the initial choice at the middle of the learning period than at the beginning. With one exception the curves for the initial choice exhibit a pronounced descent for the first stages of mastery. 3. With four animals progress in the mastery of the initial choice was correlated with the degree of success for the day, although these choices were the more difficult. In these cases the mastery of the problem as a whole was apparently dependent upon the ability of the animal to get the day's sequence started properly. With the remaining four animals, these two aspects of the problem were apparently not related. 4. All animals finally succeeded in mastering this

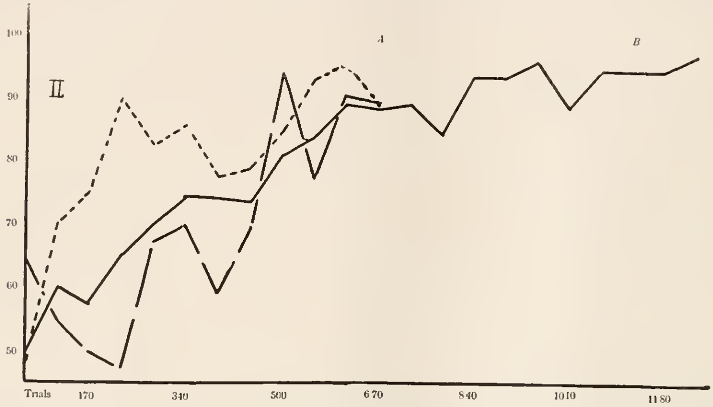

FIGURE 2.—Curves of learning. Solid line, group curve; broken lines, typical individual curves; curve from A to B, progress of group during period when control tests were given.

initial choice with a high degree of perfection. Some typical examples of these curves are given in figures 3 and 4. The solid line 1 represents the curve of learning for the problem as a whole, while the dotted curve 2 represents the course of mastery of the initial choice. Fig. 4 represents the exceptional case in which the solution of the two aspects of the problem were related and equally difficult. In fig. 3 the initial choice exhibited the greater difficulty; for some periods the two aspects were mastered together, at other times progress was antagonistic, while for most periods one problem was mastered independently of the other.

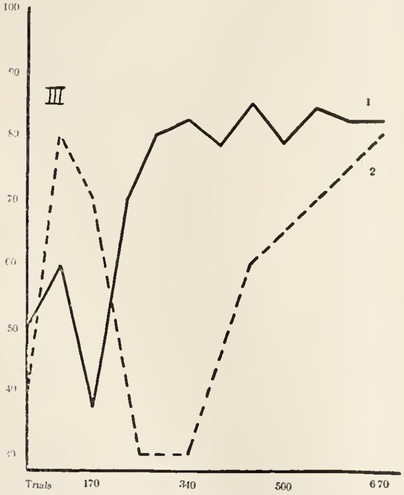

FIGURE 3.—Graph 1, individual learning curve; graph 2, curve of learning for mastery of initial choice.

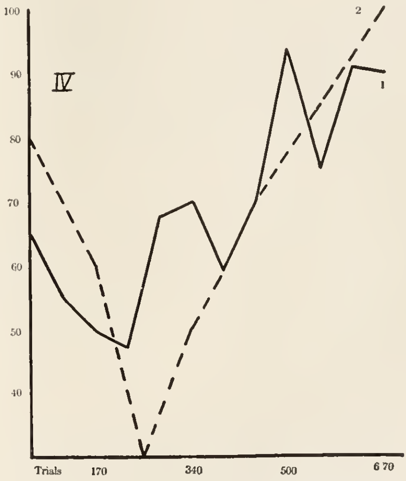

FIGURE 4.—Graph 1, individual learning curve; graph 2, curve of learning for mastery of initial choice.

Separate records were kept for the mastery of the two position habits. A comparison of the individual graphs reveals two general results. 1. Five animals found the mastery of the left position to be the easier. More correct choices of the left exit were consistently made for all stages of learning. The two positions were practically equally difficult for the other three animals. Mastery of the two habits was synchronous. 2. With four animals, the two habits antagonized each other's progress for the first half or two-thirds of the learning period. A rise in one curve was generally correlated with a fall in the other, and vice versa. The mastery of one path was made at the expense of an increased number of wrong choices of the opposite path. In the final periods of learning, however, the two habits were brought up to the same degree of perfection and progressed together. In all four of these cases the left path proved to be the easier and was mastered first. The reverse situation obtained for the other four animals. Progress in one habit was almost invariably associated with progress in the other. The two curves were thus similar in form. Typical examples of these relations are represented in figures 5 and 6.

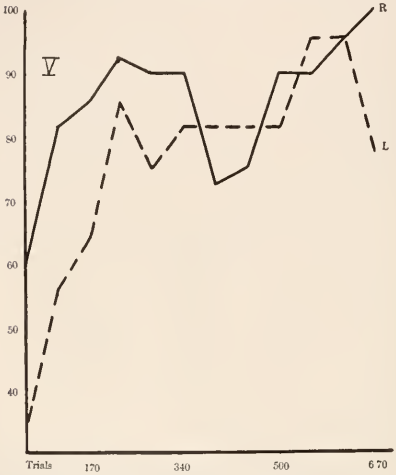

FIGURE 5.—Graphs R and L, curves of mastery of the right and left exits respectively.

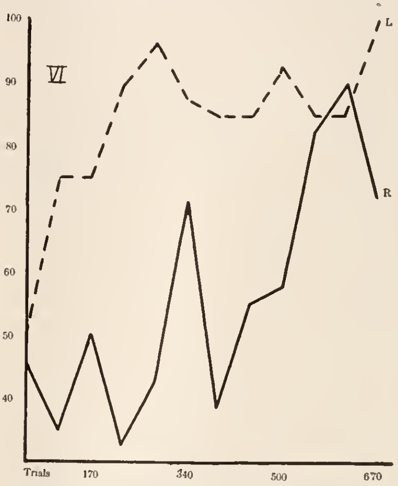

FIGURE 6.—Graphs R and L curves, of mastery of the right and left exits respectively.

The graphs L and R represent the progressive mastery of the left and right paths respectively. In fig. 6 the two habits antagonize each other's progress in the main, and the left position is the first to be mastered with any degree of perfection. In fig. 5 the two positions are mastered simultaneously, although the right habit maintained somewhat the higher degree of perfection for most stages of development.

During the solution of the problem, the animal may develop several modes of attack. 1. The rats may acquire a position preference, or they may distribute their choices equally between the two exits. A fixed preference for either of the two exits will give a percentage of 50 of correct choices and no improvement will be possible until the habit is broken. An equal distribution of choices will give a score of 50% with no improvement so long as the choices are a matter of chance. When the alternation system is mastered, the choices will still be equally distributed and a score of 100% will be attained. 2. The rats may develop the tendency either to repeat or alternate from the previous choice. An invariable repetition of the previous choice irrespective of whether it was correct or incorrect is equivalent to a position habit and it will give a score of 50% with no improvement. Alternation from the previous choice will give a score of zero if each day's initial choice was incorrect, while a perfect score of 100% will be attained if each day's sequence gets started properly. 3. The rats may also develop the tendency either to repeat or to alternate from the previous exit that gave food. The repeating tendency will necessitate a wrong alternation with a score of zero. The alternating tendency will solve the problem and give a score of 100%.

All possibilities thus reduce to two, the development of a position preference, or the acquisition of a habit of alternation and this alternating sequence of choices may or may not conform to the objective sequence. Our results were now analyzed and tabulated with the purpose of studying the development of these two tendencies.

The relative number of R and L choices, irrespective of their correctness, was determined for the successive stages of learning. The group exhibited a slight preference for the R exit for the first 100 trials. A pronounced L preference was now developed and this persisted with some degree of strength until the 500th trial, after which point the choices were equally distributed between the two exits. The L exit was consistently chosen in two-thirds of the trials for a period of 200 trials. The development of the L preference was confined to five of the eight animals, while the other three rats maintained a practically neutral attitude towards the two exits throughout the entire period of learning. The L preference began to develop somewhere in the period from the 50th to the 170th trial and it persisted for a period of 300 to 600 trials. Four of the five animals at times chose the L exit in 80% of the trials. The development of this preference may be both advantageous and detrimental to the mastery of the problem. It must certainly be detrimental in part because this habit must be broken before the problem can be mastered. The detrimental character of the habit is evident from the following facts. Each animal was ranked as to speed of learning. The three rats that developed no preference stood 1st, 2nd, and 6th in quickness of mastery. Among the five rats with a position preference those two which first eliminated this tendency were also the first to master the problem, while that animal which was the last to eliminate the tendency was also the last to complete the mastery of the problem.

The existence of these position preferences explains the relative speed of development of the two habits as previously described and illustrated in figures 5 and 6. The group of five animals that developed a preference for the left position contained the same individuals as the group that exhibited the greater progress in the mastery of the left path. The three animals that developed no position preference were the ones which mastered the two habits simultaneously. The distribution of the total choices between the two exits was practically identical with the distribution of the correct choices alone; this relation holds for the records of the group and each of the individuals. No matter how the total number of entrances are distributed between the R and L exits, the percentages of correctness for each are practically the same. In case a rat chooses the left exit 80 times in a series of 100 trials when it has developed an accuracy of 75%, the numbers of correct choices for the left and the right exits will be 60 and 15 respectively. The absence of a position preference will give 50 entrances for each of the exits in a series of 100 trials, and in this case the number of correct and successful responses will be equally distributed between the two paths. Since the percentage of successful responses is independent of the distribution of the choices, the number of correct choices of either exit must be a function of the frequency with which it is entered. In other words, the relative progression in the mastery of the two habits as illustrated in figures 5 and 6 is almost wholly a function of the position preferences which have been developed.

The rats may repeat or alternate from the previous choice and this alternation may or may not conform to the objective sequence. An analysis of the results reveals the following facts:—1. The repetitions and the alternations are practically equal in number for the first 50 trials. Evidently no animal came to the problem with a preference for either mode of choice. 2. Three rats maintained this neutral attitude for 150 trials, and then rapidly developed a pronounced preference for the alternating mode of attack. One animal immediately developed a slight preference for alternation and maintained this attitude for 400 trials, relapsed into a neutral attitude, and then rapidly developed the habit of alternation. Three animals rapidly developed a repeating preference for 300 to 400 trials, and then shifted quite rapidly to the opposite mode of attack. The remaining animal first developed a slight preference for alternation, shifted to the repeating tendency for 100 trials, and then perfected the habit of alternation in 300 trials. 3. The correctness of the choices due to repetition is a matter of chance. Each rat closely approximated a score of 50% of correct choices for every stage of learning. 4. The correctness of the choices due to alternation is at first a matter of chance. All rats approximated a score of 50% for the first 50 trials. Finally the rats learn to adapt their alternate choices to the objective series and approximate a score of 100% for this mode of attack. 5. Four rats rapidly learned the trick of adapting their alternate choices to the objective sequence. A score of 90% or better was attained in 150 to 250 trials. One of these individuals lost the trick for quite a long period and then remastered it. The other four animals at first increased their percentage of wrong alternations for 160 to 280 trials, and then quickly learned to adapt their choices to the objective series. 6. There is no correlation between initial ability to alternate and success in adapting this to the objective sequence. Of the four rats that immediately developed a preference for alternate choices, two succeeded in adapting these to the objective sequence and two did not. Of the four animals that decreased the initial number of alternate choices, two succeeded in adapting them to the given order of presentation and two did not.

Our problem thus presents four distinct difficulties which must be mastered:—1. The rat must learn to choose correctly the initial entrance for each day's trials. 2. The animal must learn to keep its choices equally distributed between the two exits, or, in other words, it must inhibit all tendency toward the development of a position preference. 3. The animal must learn to alternate its choices, and 4, it must further master the trick of adapting these to the temporal order of presentation.

The progressive mastery of the above aspects of the problem accounts for the peculiarities of the various curves of learning. An analysis of three typical learning curves into their four components will be given as illustrations.

The dotted line curve of fig. 2 exhibits the most pronounced initial rise and this rat was the first to master the problem with any degree of perfection. This animal also made the most rapid progress in mastering the initial choice, developed no serious position preference, belonged to the group which made the greatest progress in learning the habit of alternation, and was the first to learn the trick of adapting its alternate choices to the objective sequence.

Curve 1 of fig. 4 exhibits a rapid descent for 220 trials and this is followed by a normal rate of ascent until the problem was mastered. Likewise we find that the percentage of correct initial choices rapidly decreases for 250 trials and then increases at a normal rate. The animal also developed a position preference which reached its maximum strength at the 330th trial, and which was then quickly eliminated. The rat also developed a repeating preference up to the 390th trial, and then shifted very quickly over to the system of alternate choices. The percentage of correctness of the alternate choices decreased for 220 trials, and the animal then began to learn to adapt these to the objective sequence.

Curve 1 of fig 3 exhibits four aspects, an initial rise at the 100th trial, a pronounced fall at the 150th trial, a rapid rise to the 330th trial, and a subsequent plateau period. The corresponding percentage record of the initial choices is represented by curve 2 of the same figure. The animal first succeeded in choosing correctly, then failed dismally, and again succeeded. This rat also exhibited for 150 trials a position preference which was then quickly eliminated. The rat made no progress in increasing the number of alternations for 150 trials, and then practically perfected the habit in 150 trials. The curve representing the percentage of successful alternations is practically a replica of the learning curve of fig. 3.

The most important aspect of the problem is the ability to adapt the alternation to the objective sequence. The curves representing the percentages of successful alternations approximate most closely to the learning curves. Next in order of importance is the ability to alternate. The success of the initial choice is the least important factor; this fact is readily comprehensible from two considerations. The number of initial choices constitutes a very small proportion of the total, and the ability to alternate successfully depends but little upon the success of the initial choice except after the problem is practically mastered.

NATURE OF THE CO-ORDINATION

Each of the two alternating habits consists of an association between a movement and a certain stimulus. The two stimuli must fulfill at least one requirement; they must be presented in a given temporal order. Four possibilities exist:—1. The animals may be reacting in a differential manner to the two acts of adjusting the sliding doors, or to two different sensory conditions resulting from the adjustment. 2. They may be reacting to two different ways in which they are handled and placed in the starting position. 3. Each movement may be aroused by the cutaneous and kinaesthetic stimuli resulting from the previous act. This hypothesis assumes that the two acts are functionally related to each other in much the same way as are the two leg movements in locomotion. 4. The rats may be reacting to two different motor attitudes maintained during the act of feeding. The arrangement of the apparatus was such that the animals were forced to alternate between two opposite directions of approach to the food. It is possible that the body orientation involved in approach may be continued during the act of feeding, and hence that each run is preceded by a distinctive motor attitude toward the food.

The first possibility was eliminated by instituting tests in which both sliding doors were left open; in other words the rats were forced to react when the usual acts of adjustment were omitted. Again the doors were adjusted only after the choice of exits was made. Such control conditions did not decrease the percentage of correct responses.

The second possibility was tested in several ways. 1. The rats were placed in the box as usual with the exception that the head was placed at X when a choice of the left exit was demanded and at Y when the right exit constituted the correct response. The animals were thus compelled to start from two distinctive positions of such a character that a correct response necessitated a diagonal course from each position to the appropriate exit. The percentage of correct choices for the group under these conditions is represented at A in the graph of fig. 7. 2. The rats were now placed at the two positions, X and Y, in such a manner that a correct choice necessitated a direct course to the proper exit. The percentage result for the group is represented by B in the curve. 3. The animals were handled and placed in the usual position by Dr. Vincent. These results are represented in the curve at the points C. 4. The animals were subjected to normal conditions when the left opening constituted the correct choice, but whenever the right exit was to be chosen the animals were given a body orientation with the head pointing toward the right instead of to the left as under normal conditions. This orientation of the animal compelled the experimenter to place the rats in position with the left hand. The two choices are thus preceded by two distinctive methods of handling and two different orientations of the body. The results from this test are represented at the points D. 5. The rats were invariably given a head orientation toward the right instead of to the left as with normal conditions. This procedure involved a new method of handling and a new method of turning in starting for the exits. The results of the test are represented at the points E.

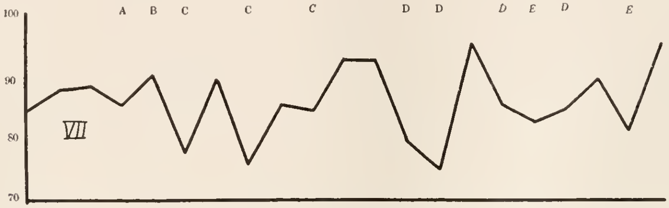

FIGURE 7.—Group curve representing the effect of the introduction of control tests.

Tests for normal conditions were interpolated among these control experiments. The records secured for these normal conditions are represented in the graph at those points not marked by letters. The value for each point of the curve represents the percentage of correct choices for the group out of 224 trials.

The following conclusions may be derived from the results of these control tests. 1. The introduction of the novel conditions decreased the number of correct choices for the group by 10%. 2. The alterations did not disturb two of the eight animals. The percentage of correct choices of the rat manifesting the greatest disturbance was lowered from 91 to 75%. No animal fell below a record of 75%. 3. The most disturbing conditions were those in which the animals were handled by strange hands and in which they were subjected to a new body orientation in starting. 4. The rats quickly adapt to these novel conditions. This fact is evident from an inspection of the graph. 5. The interpolation of these novel conditions interfered little, if any, with the progressive perfection of the two habits. At the beginning of the tests the animals had just attained a consistent group average of 85% of correct choices. At the end of the tests a record of 95% was secured. An improvement of 10% was thus attained during the period in which the tests were given. The perfection of the two habits during this period relative to the progress attained during the previous learning period is represented by the solid line graph of fig. 2. The curve up to the point A represents the progress attained during the learning period. The part of the curve between A and B represents the records secured from the tests for normal conditions which were interpolated among the various control experiments. The rate of progress during the control period is somewhat less than that obtaining for the period of learning. It is impossible to assert, however, that this decreased rate of learning is due to the introduction of the controls. 6. As previously noted the animals experienced difficulty in mastering the initial choice for each day's trials. This fact indicates that the animals were not relying exclusively upon sensory data derived from the mode of handling or the position in which they were placed in the apparatus. If such stimuli were efficacious, the first choice should have been no more difficult than the subsequent ones.

The above results prove rather conclusively that the animals did not rely exclusively upon the second class of stimuli. Neither does the slight decrease in efficiency resulting from the altered conditions prove that the rats are relying upon these stimuli in part, for any alteration of the subordinate and supplementary sensory environment may produce disturbances as readily as those aspects which are utilized as guides and controls. In other words, these altered conditions may have operated merely as sensory distractions. There are several considerations which indicate the truth of this hypothesis. The rapid adjustment to these changes is readily interpreted on this basis. The relatively poor records secured by the second experimenter were evidently due to fear. This emotional reaction was quite evident in the animal's behavior. The hypothesis is further supported by the fact that these changes did not materially effect the rate of progress in the final perfection of the habits.

The animals usually did assume and maintain a bodily orientation during feeding resulting from and characteristic of their direction of approach to the food box. However constancy of motor attitude was not the invariable rule. No attempt was made to control this factor nor were systematic records of bodily orientation taken. We are thus forced to the conclusion that the controlling and guiding stimulus to each choice consists either of the sensory aspects of the alternate act or of a motor attitude resulting from that act.

EFFECT OF INCREASING THE TIME INTERVAL

During the mastery of the problem, a period of 16.5 seconds was devoted to feeding and handling between runs. After the perfection of the association, this time interval between the two acts was gradually increased in order to determine whether the ability of the animals to make correct choices was dependent upon the length of this interval.

The results of this experiment are graphically represented by curve 1 of fig. 8. The percentages of correct choices are represented by the ordinate values while the various time intervals in seconds are distributed along the abscissa. The first four percentage values were secured for the normal time interval of 16.5 sec. All percentage values for the periods of 16.5 and 44 seconds inclusive are based upon a total of 224 trials. As the time interval is increased, the animals are given a greater opportunity for feeding, and necessarily fewer trials per day can be given. As a consequence the percentage values for the intervals of 50 to 95 seconds are based upon a total of 48 trials each. The following results are apparent from an inspection of the graph. 1. A gradual increase of the interval from 16.5 to 50 sec. exerts but little effect upon the accuracy of the act. The lowest record of correct choices for any animal for two successive days' trials was 82%. Six of the animals were able to make a record of 100% for a similar number of trials. 2. An increase of the interval up to 44 sec. did not disturb the accuracy of the act for normal conditions. A test for the normal time interval was interpolated after the group was given the 44 sec. interval. A group record of 96.5% was secured for a total of 288 trials. This value is not represented in the curve. 3. The number of correct choices suffers after a period of one minute is reached. This drop in the percentage values for the longer time intervals is not due to a diminished hunger motive as the number of trials per day was decreased from fourteen to six. The introduction of the longer intervals decreased the percentage values for the group about 10%. The lowest individual percentage record for the eighteen trials devoted to the three large intervals was 80, while the highest was 100. The decrease in the values was limited to five of the eight rats.

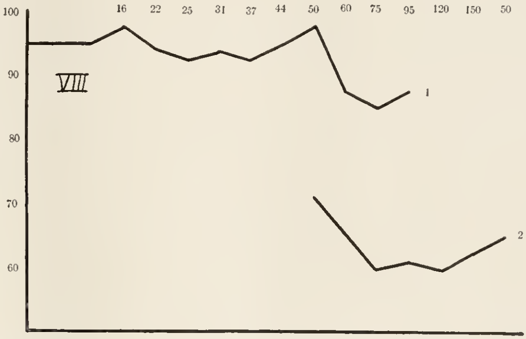

FIGURE 8.—Graph 1, percentage of correct choices for group with increasing time intervals. Graph 2, percentage of correct choices for group for large time intervals and the introduction of new conditions during the delay.

The experiment was continued with somewhat different conditions. After each trial the rats were allowed a few bites of food and then were placed upon an adjacent table. At the expiration of the given time interval, they were again placed in the apparatus for the succeeding trial. These conditions are radically different from those under which the problem was mastered. With the previous conditions the animals devoted themselves during the period of delay to the act of eating and they usually maintained a relatively constant position. On the table the rats were free to run around and react to whatever stimuli that may attract their attention. The purpose of the experiment was twofold. 1. We wished to determine the dependence of the choices upon the activities obtaining during the period of delay. To this end, we repeated the tests for the intervals of 50, 75 and 95 seconds. 2. We wished to continue the experiment with larger time intervals than the previous conditions permitted. With the new conditions the usual number of trials per day can be given even though very large time intervals are employed.

The results secured for these conditions are represented by curve 2 of fig. 8. The percentage value for the interval of 50 sec. is based upon a total of 1070 trials. The remaining values are each based upon a total of 100 trials. The following conclusions have been derived from these data. 1. The introduction of the novel conditions during the delay has decreased the percentage of correct choices by about 27%. The validity of this conclusion is readily apparent from a comparison of the two curves of fig. 8. 2. All of the animals were able to approximate a record of 70% of correct choices for the interval of 50 sec. 3. No improvement was manifested for the 50 sec. interval although the rats were tested daily for a period of 15 days. 4. The co-ordination was again disrupted for intervals greater than 50 seconds. The similarity of the two curves for the intervals of 50 to 95 seconds is striking. This fact indicates that the 60 sec. interval is a critical point. 5. Further increases beyond 75 sec. seem to be without effect. 6. The larger time intervals did not wholly destroy the functional efficiency of the co-ordinations for six of the eight animals. The group averages for these larger intervals are all at least 60%. Two rats made records of but 51 and 52% for the four large intervals. The percentage records of the remaining animals are at least 60%. The highest record was 70% and this score was made by two rats. Since these values are based upon a total of 52 trials for each rat, it is probable that some of these scores are significant. 7. The introduction of the long delays has tended to disrupt the act for the shorter intervals. The rats were finally tested again for the 50 sec. interval. Much poorer records were obtained than for the initial tests. The group record was decreased by 10%. Only four of the animals were now able to choose correctly for a score of 67% or better.

The experiment permits of the following general conclusions. 1. The guiding and controlling stimulus to each choice is constituted in part by the sensory aspects of the preceding act. A certain percentage of correct responses was obtained when all possibility of distinctive motor attitudes during the delay was wholly eliminated. Furthermore, any increase of the time interval beyond 60 sec. decreased the percentage of correct responses. 2. The rat may thus establish an associative nexus between a sensory stimulus and an act which are separated by a time interval of 16.5 sec., provided that relatively constant conditions exist during this period. 3. When an association has been established for a period of 16.5 sec., approximately one minute is the maximum time of separation of the stimulus and the response that may be obtained without disturbing their functional relation. 4. The functional efficiency of the coordination depends in large part upon the stability of the conditions that obtained for the period of delay. This fact supports the hypothesis that the guiding stimulus to each choice is constituted to a large extent by a distinctive motor attitude resulting from the previous act. The proof is not at all conclusive, however, for it is entirely possible to assume that the disruption of the act was due to the distractive influences of the novel sensori-motor conditions. 5. The efficacy of motor attitudes in the solution of the problem is indicated by the following facts. The relative disturbing effects of an increase of the time interval and the introduction of new conditions during the delay differ with animals. One may infer that some animals rely mainly upon the sensory aspects of the previous act as guides to conduct while other animals rely mainly upon motor attitudes. It is logical to suppose that those animals that place their chief reliance upon motor attitudes will learn the problem with the least effort because of the closer temporal contiguity of the stimulus and the response. As a matter of fact a positive correlation of .60 obtains between the ability to master the problem and the degree of disturbance due to the introduction of novel conditions during the interval of delay. In other words, those rats that rely mainly upon motor attitudes learn quickly and display the most disturbance when these motor attitudes are altered. On the other hand a negative correlation of .48 obtains between speed of learning and the degree of disturbance due to an increase of the time interval. Those rats that rely mainly upon the sensory aspects of the previous act in the solution of the problem are relatively slow learners and exhibit the greatest disturbance when this time interval between the stimulus and the response is increased.

FUNCTION OF VISION

The group of eight rats contained three blind animals. The records of the two groups were compared. The individual records are so variable and the numbers in each group are so few that it is impossible to make assertions with any degree of confidence. In general the group differences that exist are so small that they may well be due to chance or individual differences. Consequently the data as given justify the following negative conclusions. 1. The presence of vision did not influence the rate of learning. 2. No differences in the type of curve were apparent. 3. There were no manifest differences as to the interrelation of the R and the L habits. 4. No assertions can be made as to any differences of ability in mastering the initial choice for each day, or as to the relation between this choice and the day's success. 5. No differences were manifested in the mode of attack, or the ability to adapt the alternate choices to the objective sequence. 6. The groups did not differ as to the relative reliance which they placed upon the two sets of guiding stimuli. 7. No assertions can be made as to any differences of ability in solving the problem of increasing intervals of delay. It is of course possible that some of the above conclusions will need revision provided larger groups of animals are tested.

Two differences were detected. 1. The blind animals were somewhat the slower in movement and expended more time in making each run. The average time values per run were 6 and 7.2 seconds for the normal and the blind animals respectively. 2. In the later stages of mastery, the normal rats frequently turned immediately after entering the blocked path. The blind rats did not manifest this type of behavior. When wrong choices were made, the blind animals did not correct their mistake until actual contact with the closed door was effected. This differential behavior indicates that the normal animals frequently used visual data in reacting to a blocked pathway.

SUMMARY

All rats succeeded in learning to make alternate choices between two exits. The problem proved to be rather difficult for these animals.

The problem is a complex one consisting of four components which are stated in their order of importance. 1. The rat must learn to adapt its alternate choices to the given order of presentation. 2. The system of making alternate choices must be acquired. 3. The rat must resist the tendency of developing a position preference. 4. There is the final difficulty of choosing correctly in the initial trial of each day's test,—of getting the day's sequence started correctly.

These four aspects of the problem constitute to some extent independent difficulties in the early stages of mastery; progress in mastering one component does not necessarily depend upon the animal's ability to overcome the other difficulties. The four factors were mutually related in the case of some individuals, but there is no *necessary* dependence inasmuch as they were unrelated with some animals.

Animals differ greatly in their rate of progress in mastering each of these component elements of the problem. The curve of learning for the problem as a whole may be regarded as a combination of the four curves representing the mastery of the four components. The complexity of the problem, the independence of its parts, and the variability of the animals in mastering each part make possible a wide range of individual differences in rate and method of learning.

The final co-ordination consists of an association between each act and the sensory aspects of the preceding act as well as a distinctive motor attitude resulting from the same. The relative efficiency of the two stimuli in determining each choice varies with the individual. The problem was mastered quickest by those animals that relied mainly upon the factor of motor attitudes in making their choices. This fact suggests the hypothesis that the speed of learning is to some extent a function of the degree of temporal contiguity between the terms to be associated. Since the animals relied in part upon the sensory aspects of the preceding act, we are forced to conclude that a rat can establish an associative nexus between a stimulus and a response separated by a time interval of 16.5 seconds, provided that relatively constant sensori-motor conditions prevail during that interval.

The rate and mode of learning are apparently not dependent upon vision. Rats with vision exhibited the greater speed of movement and occasionally corrected their wrong choices in terms of visual stimuli from the closed doors.

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THE BEHAVIOR OF LIMPETS WITH PARTICULAR REFERENCE TO THE HOMING INSTINCT

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INTRODUCTION

More than casual interest attaches to the behavior of animals that possess marked homing ability and it is of importance that the detailed behavior of such forms be recorded. Certain investigators have maintained that homing is a type of behavior set apart from the ordinary reactions of animals and in an attempt to explain the homing ability have hypothecated a sixth sense or some even less demonstrable factor. No morphological foundation for such hypotheses seems discoverable and we must, therefore, look to a detailed examination into the behavior of homing animals for an explanation of the homing instinct. We need not, I believe, look for this explanation to result from some startling discovery, but rather, expect it to emerge from an apparent hodge-podge of miscellaneous facts relating to animal behavior. It is not likely that the homing instinct is peculiar to any particular type of organism but it is rather inherent in all protoplasm. In the process of evolution certain groups of animals seem to have developed the homing ability to a higher degree than have other groups, but this is true for all other types of animal behavior. In the so-called homing species, the variations in the ability of the individuals to home are so marked and the instances of homing behavior in so-called non-homing species are so numerous, that one cannot but believe that animals differ quantitatively rather than qualitatively in the possession of this instinct.

Among the invertebrate forms, the limpets are particularly interesting in connection with investigations of the homing instinct. These animals possess none but the simpler types of sense organs yet show marked ability in finding their way back, at regular intervals, to a given resting place or "home." The observations herein recorded possess only passing biological interest when taken singly but it is felt that as a whole they may be of some assistance to other observers who are interested in limpets and their homing behavior. They were made, during the winter of 1915, at which time the author was staying at the Scripps Institution for Biological Research, which institution is located at LaJolla, California.

PRESENTATION OF DATA

The rocks, on the beach to the north of the Scripps laboratory, are thickly populated with limpets belonging to three genera and to at least six species. The genus Acmea is represented by the species *patina*, *persona*, *scabra*, and *spectrum*. The two other genera are Lottia and Fisurella; of these genera one species each is common, namely, *L. gigantea* and *F. volcano*.

1. *Distribution of the limpets.*—The limpets show marked generic and specific differences in their distribution on the beach. The most common species is *Acmea scabra*, which occurs in great numbers on all the rocks of the high and middle beach. The other species of Acmea are not so numerous nor so widely distributed as *scabra*. *A. patina* and *A. persona* are found with scabra on the middle beach while *A. spectrum* is usually more abundant on the lower beach. Lottia *gigantea* occurs only in situations exposed to the main force of the waves. Specimens of *Fisurella volcano* were frequently collected from the kelp-covered rocks that are barely exposed at low tide. A large per cent of such specimens were living in the hollow halves of the deserted bivalve shells that are firmly cemented to these rocks.

2. *General behavior of the limpets.*—The movements of the limpets are largely controlled by the tides. When the tide is out, they remain practically motionless on the rocks and present no visible sign of life. With the first dash of spray from the incoming tide they begin to move and are apparently active until the water recedes once more.

3. *The clinging of the limpets.*—Limpets are completely helpless when removed from the rocks. If dropped into still water, they invariably fall with the shell side down and unless righted by some external force will remain in this position, perfectly helpless, until dead. Individuals dropped into an aquarium at first made attempts to right themselves by stretching the foot up out of the shell. They were unable to turn over, however, and after 48 hours, all were dead.

This helplessness when detached, suggests that the marked ability to survive and multiply, which limpets possess, must be accompanied by an ability to prevent themselves ever being detached. To ascertain with what force they cling to the rocks, a pair of miniature, three-clawed tongs was made from large fish hooks, and employed in pulling the animals from their attachments. The sharpened points of the claws of the tongs were hammered into knife edges so that they could be easily inserted under the edges of the limpets' shells. With the limpet attached to the rock the tongs were adjusted in such a manner, that the animal could be lifted directly from its resting place by a pull, perpendicular to the rock's surface. A spring balance, that had previously been calibrated, was hooked into the eye ends of the tongs and a steady pull detached the limpet from the rock. By noting the figure reached by the indicator of the scale just as the limpet left the rock, the pull necessary to overcome the attachment of the limpet's foot was determined.

Limpets of various sizes and species were tested with the following results. No marked specific differences in clinging power were observed, the recorded differences being directly correlated with the area of the foot of the individual.

The figures show a variation from 5 lbs., the force required to detach the smallest limpet tested, to 48 lbs. for the largest. The foot of the smallest animal was 2.2 cm. long and 1.8 cm. wide, while that of the largest was 4.3 cm. by 3.2 cm.

It was noted that the limpets need not be attached to a smooth surface, but rather the contrary, if they are to display their best clinging ability. Limpets that were attached to barnacle covered rocks seemed to cling with fully as much force as those attached to the fairly smooth, but wave eroded, rock surface. When limpets were pulled from barnacle encrusted rocks, the barnacles with which the foot of the animal was in contact were frequently detached with the limpet and remained attached to its foot. In many instances, the limpets were attached to the barnacle covered rocks in such a way that one could actually see daylight between the rather loosely set barnacle shells under the animal's foot. Even in these cases, the pull required to detach the limpet was very little if any less, than that required for the other situations and usually the limpet did not leave the rock, without bringing the barnacle cases with it. On the other hand, limpets pulled from glass plates came off with the application of about one-half the force necessary to detach them from the rocks. Calculations, based upon the clinging power of the limpets, indicate that the large Abalones (another gastropod mollusc much larger than the limpets) that are numerous along the coast of southern California can cling with a power equal to 1100 pounds weight. One who has attempted to pull them from the rocks may well credit them with this great adhesive power.

4. *Reaction of limpets to environmental factors.*—A large number of readings were was taken as to the position which the limpets assume on the rocks, in relation to the current made by the waves, to the pull of gravity, and to the direction of the sun's rays. The readings were taken daily for three weeks. The following table summarizes the results.

Reaction to—	Positive	Negative	Indifferent
Current	450–51%	321–36%	117–13%
Gravity	334–54%	203–33%	73–13%
Light	285–37%	266–36%	199–27%

The figures indicate a strong positive reaction to current and gravity but none to the light. It is readily noted that limpets do not occupy the sunny sides of rocks but this is probably a negative reaction to temperature rather than to light. Experiments with light gradients will probably indicate a selection of a medium light upon the part of these limpets. In the above experiments the reaction was to direction of rays rather than to intensity since the orientation of the animals, i.e., whether facing toward or away from the sun, were the only data recorded.

5. *The homing instinct.*—Observations, continuing in some cases for a little over a month, were carried on, to determine the daily relation of the different species of limpets to a given resting place on the rocks. The idea was, first, to determine whether or not any or all of the species possessed a definite

homing ability, and second, to ascertain something as to the nature of such ability should it be present.

All of the limpets under observation were found to move about, at periods of high tide only. The movement began with the first wetting from the incoming tide, and proceeded more or less continuously, till the retreating water left the animals high and dry once more.

About 30 limpets, representing four species of Acmea and the one species of Lottia, were marked by filing Roman numerals into their shells. This method made it necessary to mark the animals but once, for the grooves could be filed quite deep into the shells without injuring the animals in the least.

The limpets were chosen, so that all the possible situations were represented. Some were on horizontal rocks, some on vertical ledges; some were exposed, some were not, etc. The spot on which the limpet was resting, on the first day of observation, was enclosed in a small rectangle scratched into the rock and alongside this rectangle the roman number which the limpet carried was also filed into the rock. From day to day the location of each limpet was determined by referring it back to this numbered rectangle. The daily positions were plotted on squared paper and the resulting graph, together with the field notes, constitutes the permanent record of the limpet's activities. The graphs that follow will furnish an idea of the behavior of the different species of Acmea, during the period of observation.

Figure 1 indicates the wanderings of an individual of the species *Acmea spectrum*, during a period of 27 days. It is at once evident that this animal did not habitually return to any given spot on the rock, when the tide retreated. It will be noted further that there was even a tendency to change localities. This individual was situated on a flat rock, where the waves washed it much of the time.

The readings represented in Figure 1 were taken but once a day and it soon became obvious that there was considerable to be learned by observations made at more frequent intervals. To check up this point a number of days was spent taking hourly observations upon individual limpets. Figure 1A shows the result of hourly readings upon the individual referred to in Figure 1. Figure 1A, from its appearance, might represent a series of 5 consecutive readings taken from some part of Fig. 1,

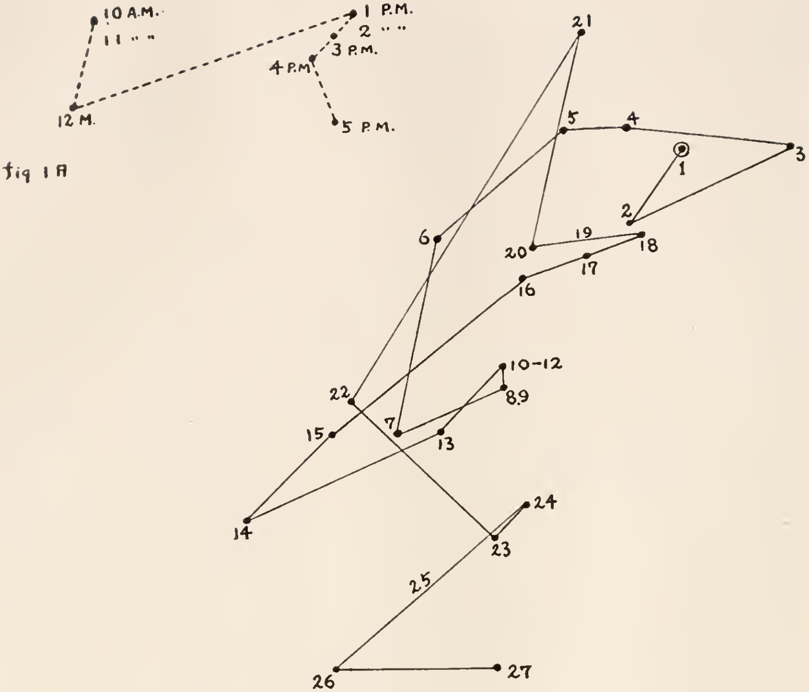

Fig. 1.

FIG. 1.—Graph of the movements of a non-homing individual of *Acmea spectrum*. Observations made once a day for 27 days.

FIG. 1A.-Graph of the movements of the limpet whose path is shown in Fig. 1. The movements shown in Fig. 1A took place on the 15th day. Readings hourly.

yet it is actually part of the path travelled between the 15th and 16th readings. It is evident that the limpets move about a great deal more than the graph (Fig. 1) would lead us to believe. However, the fact remains that this particular limpet showed no signs of homing, during the period of observation.

Figure 2 indicates the behavior of another individual of *Acmea spectrum*; this individual was situated upon the same flat rock with the individual discussed above and several times the two animals were but a few inches apart. Figure 2, however, shows a very different type of behavior from that indicated in Fig. 1.

The limpet, whose path is traced in Fig. 2, shows a marked tendency to return to some particular spot, after its daily wan-

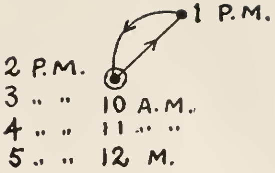

fig. 2A.

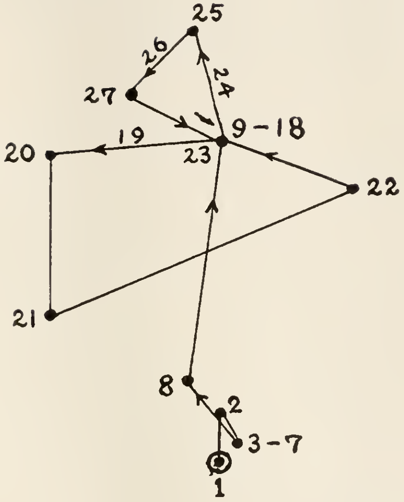

fig 2

FIG. 2.—Graph of the path followed by an individual of *Acmea spectrum* during a period of 28 days. Readings once a day.

FIG. 2A.–Shows the extent to which the same limpet moved during a seven hour period on the 14th day.

derings. During the 28 days over which the observations extended, two principal spots were occupied. Both were small depressions in the rock surface, into which the shell of the limpet fitted rather snugly. Figure 2A indicates the extent of this animal's movements during a seven-hour period of observation on March 9, which was the 14th day shown in Figure 1. Note that the limpet left the depression for only one hour and that during this time it moved out and back, along a path which represents an egg-shaped oval.

The other species of Acmea showed the same type of behavior as that indicated for *spectrum*; they showed also, the same wide variation in the behavior of different individuals. Figure 3 is a graph plotted from the data furnished by an individual of *Acmea scabra*. This individual was located on a vertical face of rock and was subjected to the direct dash of the waves.

It will be noted that the animal whose behavior is indicated in Fig. 3 was found in the same spot from the 5th to the 12th day and then, after moving about for four days, settled down again and on the 30th and last day of the observational period was still to be found in this second resting place.

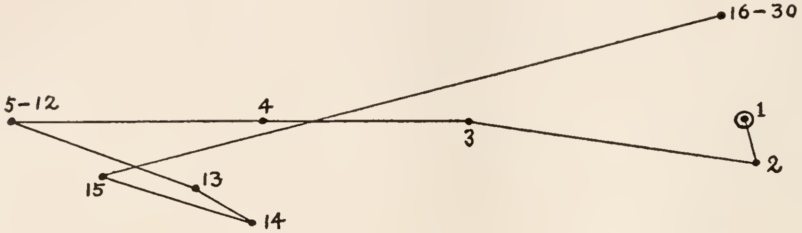

fig. 3.

Fig. 3.—Graph of the movements of an individual of *Acmea scabra*. Readings once a day.

The foregoing experiments indicate that the limpets of the genus Acmea possess a rather definite homing instinct which is displayed by certain individuals more than by others; the other data serve to confirm this view.

The species *Lottia gigantea* was found to be a very consistent homer with the individual variation reduced to a minimum. Seven individuals of this large species were marked and observed daily for 25 days. These animals were located on the exposed side of an immense boulder, and were subjected to the direct influence of the incoming waves very soon after the turning of the tide. The exposed position made observation of actual movements rather difficult, for like the other species, *Lottia gigantea* moves only when moistened by the waves.

The low-tide observations upon the seven individuals of

Lottia gigantea showed that without exception, these limpets returned daily, each to a given depression or other recognizable spot on the rock's surface. The observations on the limpets while they were moving, i.e., while the tide was coming in, showed that they left their resting places very soon after the first dash of spray had thoroughly wet them, and that they crawled about continuously as long as the observations were continued. A given individual usually left its resting place in the direction in which it was headed. It would now crawl across the surface of the rock, which was usually thickly covered with barnacles. The path taken was not straight away from the homing point but curved either to the right or to the left. After going a certain distance, usually but 5-6 inches at first, the limpet would turn almost around and after completing the other side of an oval, such as is shown in Fig. 2A, would be back at its resting place. Instead of settling down, however, the animal usually started out immediately upon another journey, which was likely to be longer than the first. From all that could be seen this procedure was kept up; each successive journey was longer than the last and on each subsequent trip the path became more and more irregular until the animal appeared to be merely wandering about in the vicinity of its resting place.

The greatest distance that any animal of this species was found from its home, was 16 inches. This individual was still 12 inches away, when observations had to be discontinued, but it was found at home as usual the next day.

No experiments were performed to determine the ability of these limpets to return to their resting place when transferred bodily to a distance, though there can be little doubt but that they would be able to do this to a limited extent, just as has been shown by Morgan for certain species which he has unfortunately failed to name.

In general, the writer was impressed with the fact that the limpet offers a much easier subject for the investigation of the homing instinct than is presented by the highly motile forms, such as the insects and birds, and at the same time it seems possible that in the investigation of the instinct which guides the limpet over its few square inches we may find a clue which will help us to explain the ability that enables birds to orient themselves over hundreds of miles.

LITERATURE FOR 1916 ON THE BEHAVIOR OF THE LOWER INVERTEBRATES

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In studying the effect of different electrolytes and cane sugar on rheotaxis in Asellus, Allee (1, 2) finds that in many respects the substances used affect the positiveness of the rheotactic reaction in the same way that they affect many other physiological processes. The antagonism between KCl and $CaCl_2$ is particularly well marked. The former increases and the latter decreases the percentage of positive reactions and shows a wholly similar effect on the rate of metabolism as measured by resistance to the cyanides and production of CO_2. The conclusions are based on experiments on over a thousand individuals.

Allen (3) gives some notes on the migrations, etc., of the spiny lobster, *Panulirus interruptus.*

In a study of the action of Schumann rays on living organisms, Bovie (4) gives an account of the response of certain amoebae and infusoria to this region of the spectrum.

The Journal of Animal Behavior (5) publishes a translation of Buddenbrock's "Die Tropismentheorie von Jacques Loeb" (*Biol. Cent.*, **35,** 481-506). The original article was noted in this review for last year.

Attention is called to Cary's (6) study of the influence of the marginal sense organs on the rate of regeneration in *Cassiopea xamachana.* A preliminary summary of this work was given in this review for last year.

Crozier (7) is of the opinion that the behavior of *Holothuria captiva* when illuminated on two sides is such as to show "that photic stimulation in this animal depends upon the amount of light falling upon the sensitive surface, and is independent of the angle of incidence." In working on *Stichopus moebii* he (8) finds that the mechanism for the pulsation of the cloacal chamber is locally contained, i.e., within the cloaca. He then takes up a study of the relation of certain chemicals, temperature, etc., to this rhythmic pulsation. The same author (9) gives a note on the behavior of the barnacle *Conchodermata virgotum* and another (10) on the immunity coloration in the nudibranch, *Chromodoris zebra.*

In studying the feeding habits of certain pelagic copepods, Esterly (11) finds that the head and appendages of *Calanus finmarchicus* produce water currents which carry floating particles toward the mouth. These currents are directed chiefly by a trough-like arrangement of the bristles of the anterior maxilliped. The particles are formed into a pellet which is held behind the mouth and from where it is passed into the oesophagus. The author then takes up a study of the various food forms found in the digestive tracts of various copepods.

Grave (12) takes exception to Kellogg (*Jour. of Morph.*, **26,** 625-701), who is working on the feeding of Lamellibranchs comes to the conclusions that " Volume alone determines whether the collected foreign matter that reaches the palps shall proceed to the mouth or shall be sent from the body on outgoing tracts." Also, as corollaries to this conclusion, that a Lamellibranch can feed only in comparatively clear water, can make no separation or selection of food particles, and has no mechanism for the reversal of the effective beat of the cilia. Grave gives some experiments on Ostrea which tend to show that they can feed in water which contains a large quantity of sediment, etc. He then collects certain evidence on other animals which shows that they can make a selection of food by a control of the beat of the cilia and suggests that the same may hold in the case of Ostrea. Kellogg (16) answers this criticism in a polemic entitled " Opinions on Some Ciliary Activities."

Jordan (13), in a study of the irritability of the muscles and the influence of the nervous system on the musculature of certain holothurians, gives a description of certain reactions of these animals.

Kanda (14) finds that the marine snail *Littorina littorea* is negative in its reaction to gravity, but that this reaction is influenced by the fact that the animal is also negative to light. The author finds that in sea water the angle of inclination (to the horizontal) of the surface on which the snails move, has a marked influence on the percentage of positive and negative animals,—the larger the angle, the larger the number of negatively geotropic animals. The presence of air or sea water, the presence of direct sunlight, and the character of the surface on which the snails move, all have some effect on the reactions to gravity. "From the experimental results which the writer has obtained, he concludes that neither the mechanical theory, nor the pressure theory, nor the resistance theory is adequate to explain the phenomenon of the negative geotropism of *Littorina littorea* but a physiological one, that is, the statocyst or statolith theory. This theory is the more likely since these snails have statoliths. The writer, however, has no direct evidence, at present, in favor of the statolith theory." A similar conclusion (15) concerning the statolith theory is reached after a study of the reactions to gravity of certain freshwater snails.

Lankester (17) gives certain arguments against the conclusion, set forth by Carpenter (1874) and Heron-Allen (1915), to the effect that the behavior of the Foraminifera is evidence of intelligence in these organisms.

In continuing their work on the relative efficiency of various parts of the spectrum for the photic reactions of plants and animals, Loeb and Wasteneys (18) give the following regions of the spectrum as being the most efficient for the following organisms: *Eudendrium ramosum*, 460-480$\mu\mu$; *Euglena viridis*, 460-490$\mu\mu$; *Arenicola larvae*, about 495$\mu\mu$; *Chlamydomonas pisiformis*, about 535$\mu\mu$; *Balanus eburneus larvae*, 560-578$\mu\mu$. These results were obtained by subjecting the organisms simultaneously to two beams of monochromatic light from different directions and then comparing their distribution in the two beams.

Löhner (19) has made some feeding experiments on leeches by letting them attach themselves to a piece of fresh animal hide which has been fastened to the end of a tube containing blood. After the animals have thus attached themselves, in a normal manner, the blood in the tube is removed and various solutions substituted. In experimenting with the so-called four types of gustatory solutions (salty, sweet, sour, and bitter) the author finds that the animals show a "detaching" or "repulsion" reaction at the following percentage solutions: Sodium chloride 7%; Cane sugar 5%; Quinine sulphate 0.08 to 0.1%; Hydrochloric acid 0.09 to 0.1%; and Potash 0.08 to 0.9%. No such reaction follows from pure water.

Following a description of the eye-spot of *Gonium pectorale*, Mast (20) gives an account of the process of orientation to light in this organism. Orientation is direct (the colonies never turning in the wrong direction) and in positive colonies it is brought about by an increase in the activity of the flagella of the zooids on the side away from the light. This is held to be dependent upon the time-rate of change of illumination on the tissue which is sensitive to light.

Mast and Lashley (21) find that there is no continuous production of a feeding-cone in free-swimming Paramoecia, Stentor or Spirostomum. The water sucked toward them is through so short a distance (probably not over twice the length of the cilia) as to make such currents of no appreciable value in testing unfavorable environment ahead of the specimen. The feeding-cone is produced only under special conditions.

Mast and Root (22, 23) find that the pseudopods of *Amoeba proteus* in forming a food vacuole about a Paramoecium sometimes come together before they are fully extended, thus cutting the latter in two. The authors estimate that if this process is due solely to a change in the surface tension on the surface of the Amoeba it would have to be higher than 383 dynes per cm.^{2} at the very least and that it probably would have to exceed 1,118 dynes per cm.^{2} As the surface tension of protoplasm is only about 50 dynes per cm.^{2}, they conclude that if surface tension plays a part in the division of Paramoecium it is a very insignificant rôle.

Maupas and Seurat (24) give a note on the copulation of certain nematodes.

As a result of a study of certain reactions of *Cassiopea xanachana*, Mayer (25, 26, 27) gives some interesting suggestions as to the nature of nerve conduction in this organism.

Mendelssohn (28) finds that a leucocyte, in response to the stimulation of an electrical current, so changes its form as to produce one large pseudopodium which is always directed towards the cathode.

Metalnikov (29, 30) finds that the length of time that a given food vacuole will circulate in the body of Paramoecium is very variable. According to him this variability depends upon three factors: (1) The character of the specific stimulating substance, i.e., the character of the food substance; (2) variations in the external medium; (3) the internal state of the organism.

Moore (31) maintains that Mast, in his work on *Gonium pectorale* (reviewed above) in which he holds that orientation to light is brought about by the increased activity of the flagella of the zooids furthest from the stimulated side, does not take into account the possibility that orientation may be brought about by the unequal activity of the two flagella of each single cell. The author's criticism is based on Moore and Goodspeed's study of the orientation of Gonium under the influence of a galvanic current.

In a study of the reaction of *Lumbricus* under the influence of a galvanic current, Moore and Kellogg (32) find that this animal at first directs both the anterior and posterior ends toward the cathode, thus assuming a horse-shoe shape. Owing to the fact that the anterior end is more active than the posterior, the worm ultimately succeeds in reaching the cathode. The author is of the opinion that these reactions are in accord with Loeb's theory of galvanotropism.

Parker (33, 34, 35, 36, 37, 38) and Parker and Titus (39) have done some very interesting work on the reactions and structure of certain sea-anemones. This work constitutes a valuable contribution to the neuromuscular physiology of this group. It is, however, too extensive to more than mention in this review.

Rabaud (40) gives an account of the occurrence of the death-feigning reflex in a number of insects and myriapods. He (41) also gives a note on the nature of this reflex.

In a study of the relation of the body temperature of certain cold-blooded animals to that of their environment, Rogers and Lewis (42) find that the earthworm quickly adjusts itself to the temperature of a rapidly circulating environment while the clam does so less rapidly. After these animals have so adjusted their body temperature, it shows a very close agreement to the temperature of the given environment.

Schaeffer (43), in studying the food reactions of two species of Amoeba finds that, "A hungry amoeba will eat the same carmine grain several times in succession, but with each eating the grain becomes less attractive, until it is refused." This refusal, he holds, is very likely due to some change in the grain of carmine as a new grain is generally eaten if presented to the animal. The animal usually rids itself of the carmine very quickly, by a more or less complete reversal of the direction of its movement. Grains of carmine are sensed by the Amoeba at a distance of at least 100 microns. The animals have a similar power of sensing egg white, uric acid and India ink at a distance. Daylight, acting continuously, has no effect on the food reactions. There is no way of predicting the size and shape of the food cup from the stimulating object alone. The author is of the opinion that the ectoplasm and endoplasm (of the granular species studied) react to such things as carmine in an opposite manner, the former being positive and the latter negative. In another paper the author (44) gives an account of the behavior of Amoeba to glass, carbon, tyrosine, egg albumen, peptone, etc.

Torrey (45) gives an essay on the physiological analysis of behavior.

Walton (46) finds that in *Paramoecium caudatum* there is an increase in the rate of locomotion in response to an increase in illumination. In animals from non-conjugating lines, 85% gave this response, whereas only 55% of those from conjugating lines showed it. This response to increased light intensity is only gradually effected. The response of a given specimen is the same to a given illumination irrespective of the light intensity to which the animal has been previously exposed, provided the specimen is given time to adjust itself to the new intensity. As has been the case with previous investigators, no evidence was found of a directive or orienting effect produced by the light.

According to Wenrich (47) *Anodonta fluviatilis* is sensitive to very slight decreases but not to increases in illumination. Such stimulation generally results in the closing of one or both siphons (seldom in closing the valves); the exhalant siphon being more sensitive than the inhalant. In continuing his work on some 18 marine species of bivalve mollusks, the author finds three classes: " (a) Those sensitive to both increase and decrease in light intensity (e.g., Mya); and (b) those sensitive to decrease only (e.g., Pecten); and (c) those sensitive neither to decrease nor to increase (e.g., Cumingia)." There is a perfect correlation in these species between sensitivity to light and the presence of pigment in the epithelium of the sensitive area. *Pecten gibbus* shows a vigorous reaction by closing the valves in response to an upward moving white card over a black background. As the upward movement of the card in this case involves an increase in light intensity and as Pecten shows typical reactions only to decreases in intensity, the author is of the opinion that these experiments show that the eye of Pecten may form an image.

Willis (48) finds that fragments of *Amoeba proteus* which contain a nucleus exhibit essentially the same type of locomotion and orientation to light as do normal specimens. In enucleated fragments, however, locomotion is very imperfect and there is no evidence of orientation to a horizontal beam of light. The author is of the opinion that this regulatory influence of the nucleus is " brought about by some sort of an influence upon the attachment of the organism to the substratum."

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LITERATURE FOR 1916 ON THE BEHAVIOR OF SPIDERS AND INSECTS OTHER THAN ANTS

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TROPISMS AND RELATED PHENOMENA

Winn (119) thinks that certain butterflies exhibit phototropisms.

A trap net, with a bright lantern as a lure, was hauled across a field on a slowly moving wagon. A much larger variety of insects was captured than were enticed into stationary lure nets. Hence Holloway (48) concludes that a moving light has a greater attraction for insects than one that is fixed.

Runner (90) describes experiments upon the effects of roentgen rays on the cigarette beetle.

Richardson (86) finds that the house-fly is attracted by both ammonium hydrate and ammonium carbonate. He also notes (85) that the odor of ammonia attracts a varied dipterous aggregation; and that all of the species thus responding are known to spend at least part of their lives in some animal excrement. Since practically all animal excrement gives off ammonia, he concludes that it is probably the ammonia gas which attracts flies to manure.

In the behavior literature of today, the tropism hypothesis holds a prominent place. There have been protests against its universal application; but, so widespread is the impression that the complex acts of insects can be resolved into tropisms that these protests are popularly considered the anthropomorphic effusions of non-critical minds. Each year the number of students who are unwilling to subscribe unreservedly to the tropism hypothesis increases. This year Pictet (79), after a critical analysis of numerous experiments, concludes that the locomotions of insects are not phototropisms. According to him: "The tropism theory does not harmonize with the variety of ways an organism responds to a given stimulus. . . . It has not been demonstrated that the ascending and descending flights of insects are determined by the direction of the rays of light; on the contrary, their movements appear to be regulated by voluntary acts, which are induced by physiological needs, fright, interest, habit, search for the female, etc. . . . Insects do not orient themselves towards either natural or artificial light in response to a physico-chemical force exerted by the rays of light, but by voluntary and conscious acts aroused by various conditions in the environment. . . . Responses to heat and cold are not tropisms, but reactions to sensations."

FEEDING AND HUNTING BEHAVIOR

Baker and Turner (6) describe the feeding habits of the green apple aphis; Barbey (8), of the larva of the long-horned beetle *Cerambyx heros*; Brittain and Godderham (12), of *Depressaria heraclina*; Clausen (14), of some Californian Coccinellidae; Cory (17), of the Columbine leaf miner; Cushman (22), of the apple red-bugs; Hayes (41), of the maize bill-bug; Herrick (43), of the cherry-leaf beetle; Hungerford (49), of Sciara maggots; Osborn (70), of several Maine leaf hoppers; Schoene (92, 93), of the seed-corn maggot and of the turnip maggot; Warren (113), of the Hawaiian dragon flies; and Whitmarsh (117), of *Apateticus maculiventris*.

Sanders and Fracker (91) find that the May beetles of Wisconsin feed upon the roots of plants and the fragments of the same; but that they will not eat moist bran nor flour paste. They feed only during the heat of the day; but there is no daily migration such as cut worms have.

Watson tells us (114) that the noctuid moth, *Anticarsia gemmatilis*, which feeds on the kudxy vine and velvet beans, forages continuously both day and night, stopping only to moult.

Essig (28) mentions a moth which feeds upon coccids.

According to McGregor (63), the privet mite feeds upon privet, Boston ivy, golden rod, palm, orange, lemon, etc.

Davis and Satterwait's investigations (23) show that the true army-worm feeds at first on its egg shells; later upon the parenchyma of the corn leaf and finally upon all the tissues of the leaf.

Paddock (72) informs us that the turnip louse feeds upon turnips, radishes, mustard, rape, collards, rutabagas, cabbages, kale, kohl-rabi, beans and lettuce.

Tower's experiments (105) demonstrate that the parasitized caterpillar of *Cirphis unipuncta* eats half as much as the normal larva.

Felt (30) finds that the feeding habits of the codling moth vary with the season. The early brood bores deep; the later keeps near the surface of the fruit.

Sell (94) has experimentally demonstrated that the 12-spotted cucumber beetle can change from an exclusive diet of one kind to a different menu, without being injured.

In 1843 Hutton[1] described the feeding habits of a large false-spider which he claimed was carnivorous. The blood-sucking habit is so universal among the Arachnida that J. H. Comstock doubted the correctness of Hutton's statements. He writes:[2] "Captain Hutton states distinctly that the *Galeodes* observed by him consumed an entire lizard except the jaws and parts of the skin. Other instances in which solpugids are supposed to have eaten their prey are given by Rev. J. J. Wood, in his 'Natural History Illustrated,' and quoted by Murray. Still, it is believed that solpugids take only liquid food, which they suck from the bodies of their victims." Turner (110) has demonstrated that the solpugids are carnivorous. Our American form, aided by the scissors-saw-like movements of its powerful jaws, pulpifies and devours all parts of captured insects except the chitin. Normally our form feeds only on live prey; but it may be caused to eat dead insects, by artificially inducing such insects to move.

MATING BEHAVIOR

Rohwer (89) discusses the mating of saw-flies; Somes (100), of the clear-winged moths *Seisia rileyana* Dry. and *Cassida solani* Boh., and Watson (114), of the noctuid moth *Anticarsia gemmatilis*.

Baker (6) states that the green apple-tree aphis mates within two days after reaching maturity and remains in coitu twenty-five minutes.

Hutchison's experiments (50) show that the house-fly mates as early as the first day after emergence and as late as the forty-seventh.

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Although the organization of termite society resembles in many respects that of the ants and bees, yet their mating behavior is quite different. According to Snyder (99) the sexual relations of termites is continuous. Copulation is repeated at regular intervals for several years.

The advent of the tropism hypothesis induced students of behavior to look upon the hovering of insects as a tropism, usually an anaemotropism. In 1908[3] it was demonstrated that the hovering of one species of mining bees is a mating device. In 1911 Perez[4] reported observations which induced him to conclude that the hoverings of several species of flies are preliminary to mating. Records of the field work of Turner (110A) on the ant *Lasius niger* and of Rau (82) on the solitary bee *Colletes compactus* show that the mating of both of these forms is preceded by a riotous sun-dance of the males. Occasionally females appear in the midst of the dancers. Then certain males drop out and mate. Apparently, in many cases, we must look upon the hoverings of insects, not as tropisms, but as prenuptial dances of the males.

According to C. L. Turner (111): "1. Movements preliminary to copulation are fairly constant in each group of Orthoptera and vary from simple (Mantidae, Phasmidae and Acrididae) to complex (Blatidae, Gryllidae, and Locustidae). 2. There is sex discrimination in the males of all forms. The female plays an aggressive part and displays discrimination of sex in some groups while in others she is absolutely passive. 3. There is a typical mode of copulation for each family of the Orthoptera. In the Mantidae, the Phasmidae and the Acrididae there is a superposition of the body of the male. In the Blatidae and Gryllidae there is a superposition of the body of the female. In the Locustidae there is an end to end copulation. 4. Families represented by the least number of sub-families are highly specialized; while those represented by the largest number of subfamilies have a generalized type of reproductive behavior. 5. A comparison between a classification based upon the reproductive behavior and one based upon paleontological evidence shows a striking agreement and suggests that the different types of reproductive behavior have been fairly constant since their origin."

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[4] Sur quelques Particularités curieuses du Rapprochement des Sexes chez certains Diptères. *Bull. Scientifique de la Belgique*, 7th Series, vol. XLV, pp. 1-14.

MATERNAL BEHAVIOR

Baker and Turner (6) describe the oviposition of the green apple-aphis; Gruppy (39), of the syrphid flies; Harris (40), of the beetle *Bruchus*; Hayes (41), of the maize bill-bug; Knab (59), of *Dermatobia hominis*; Snyder (99), of the termites; Whitmarsh (117), of *Apateticus cynicus*; and Turner (111), of several Orthoptera.

Miller (66) describes, in detail, the method by which *Megastigmus spermotropus* slowly forces her ovipositor through the cone of the Douglas fir, lays her eggs and then withdraws the ovipositor.

Evans (29) informs us that, as a rule, the house-fly does not breed in garbage, although that is one of its favorite feeding places.

Rau (82) discovers that *Calliopsis nebraskaensis* Cfd., a solitary bee the nests of which form large colonies, keeps the entrance of its nest closed.

Pierce notes (81) that the weevil, *Polydesmus impressifrons*, deposits her eggs, in masses of from 20 to 80, under the loose bark of the willow, the poplar, the birch, the apple and the pear.

Urbahns (112) states that a parasitic fly, *Habrocytus medicagnis*, thrusts her ovipositor through the walls of the seed-pod of the alfalfa into the watery seed and lays her eggs upon the larva of a chalcid fly.

Smith (98) observed a parasitic Hymenopteran, *Perilampus hyalinus*, lay its eggs on the leaf of the oleander. The newly hatched larva is well supplied with hooks. It creeps about over the leaf, then stands erect, hooks itself on the first chrysopa larva that passes and bores into it.

In a series of seventy experiments, conducted on flies placed in solitary confinement as soon as they emerged, Hutchison (50) finds that the period of preoviposition of the house-fly varies from two and a half to twenty-three days, dependent upon the temperature, the humidity, and the kind and quality of the food.

McGregor (63) states that the privet mite oviposits about twenty eggs in either an abrasion, or a depression, or in old moulted skins.

Rau (83) describes in detail the nidification of the mud-wasps *Scleiphron caementarium*, *Chalybion caeruleum*, and *Trypoxylon* *albitarsis*. He is convinced that Ashmead is in error when he claims that the last wasp mentioned uses the abandoned nests of the two former.

Turner (110) finds that an American false-spider, *Eremobates formicaria*, constructs her burrow much in the same manner as does the Indian *Galeodes*. In the lower portion of the burrow the milk-white eggs are deposited. The Indian form rests quietly among the eggs and later guards the newly hatched young from harm. The American form leaves her eggs unguarded, excavates a new burrow each night, and lays a second batch of eggs before the first has hatched.

The European wasp, *Methoca ichneumonides*, gives a tiger beetle larva an opportunity to seize her and then stings the larva and deposits her egg upon it. In an American form, *Methoca stygia*, studied by him, Williams (118) did not find any evidence of the wasp waiting for the larva to seize her. The wasp enters the burrow, stings the larva, lays an egg upon it, and then fills the burrow with sand.

Pellett (77) noticed that a paper wasp, *Polistes metricus*, Say, lays an egg almost daily upon the side of a cell, and that the mother spends most of her time feeding the young upon kneaded mosquitoes. The investigator captured mosquitoes and, after kneading them, gave them to the larva to eat. As long as the mother was living, she would remove the poorly kneaded mosquitoes, reknead them and eat them herself or else feed them to some other larva. In the absence of the female, he found it possible to raise the larvae upon these man-kneaded mosquitoes; but, the worker wasps thus raised would not nurse the remaining larvae.

According to Belsing (9), the pecan twig-girdler begins her egg-laying activities by girdling a twig. Although the branch is seldom cut through, yet its own weight usually soon severs it. On the twig the insect makes an incision, with her jaws, at the base of a leaf bud. The incision is excavated by the ovipositor, an egg deposited therein and the whole sealed with a black, gluey substance which is discharged by the ovipositor. With her mandibles, she then makes a number of small transverse incisions below the point where the egg has been laid. This causes the bark on drying to raise like a blister and not crush the egg.

Aquatic Lepidoptera are rare and almost no attention has been paid to the American forms. Recently Welch (116) has given a description of the morphology and behavior of two forms studied by him. In both species the mother lays the eggs upon submerged portions of water plants. Laboratory experiments demonstrate that in the case of *Nymphula maculatis* Clem.: " (a) Eggs are invariably deposited at night. (b) Eggs are invariably placed about Donacia (chrysomelid beetle) egg holes when the latter are available. (c) Oviposition may extend over five successive nights. (d) One female may use several Donacia holes before oviposition ceases. (e) Maximum number of eggs laid by a single female was 617. (f) In the absence of Donacia holes or other similar punctures in the water-lily leaves, oviposition was usually delayed but ultimately resulted in the deposition of small egg masses on the lower sides of the leaves at the margins. Egg masses were deposited about artificial punctures and incisions of various sizes and shapes, the dimensions of which apparently had little to do with the selection."

HIBERNATION

Cosens (19) mentions the hibernation of the lady-bird beetles of Canada.

Coad (15) finds that the pupa of the wild-cotton weevil hibernates in the bolls of *Thurbergia*.

Osborn (70) gives a list of the leaf hoppers that hibernate in Maine.

Sell (94) could find no experimental evidence that the 12-spotted cucumber beetle hibernates.

Our literature on the hibernation of flies has been augmented by articles by Ashworth (4) and Dove (25). The latter investigator finds that, in Texas, the pupae and the larvae of the house-fly overwinter in naturally accumulated manure piles. Throughout the mild winter weather adults occasionally emerge from those piles to which fresh manure is continually added. In the spring large numbers emerge.

ECOLOGY

In a paper too well filled with good things to permit of an adequate review in the limited space of this article, Adams (1) discusses the ecology of prairie and forest invertebrates.

Patch (74) contends that the most important problem in the ecology of any aphid is, " Does it migrate ?"

In his investigations of aquatic Lepidoptera Welch (116) studied both *Nymphala macularis* Clem. and *Nymphala iccualis* Wlk.; but, most of his time was devoted to the former. The larva cannot swim; its sole method of locomotion is by crawling. In both species case-making is a constant larval activity. The case is constructed out of bits of the leaves of the food-plants. This case serves as a protection and as a float.

LETISIMULATION

It is well known that the coccinellid beetle *Epilachna borealis*, when disturbed, folds its antennae and legs against the body, ejects small drops of liquid from its femoral articulations and feigns death. What is the nature of this excretion and how is it expelled so quickly ? McIndoo (64) has demonstrated that this " reflex bleeding " is a true reflex, that the fluid is secreted by hyperdermal glands, that it is ejected through groups of pores situated on and adjacent to the articular membrane, and that its ejection is accomplished by putting the gland cells under high blood pressure.

DuPorte's (27) description of the death-feigning of *Tychius picirostris* harmonizes with the accounts of the letisimulations of other invertebrates as related by several recent investigators. (1) There is much individuality. (2) There is no relation between the intensity of the shock and the duration of the feint. (3) It is impossible to prolong the feint indefinitely by means of repeated stimulations. (4) The animal may be much mutilated without being aroused from the feint. He thinks that the physico-chemical reaction responsible for the manifestation of the death feint is of the same nature as that which calls forth the thigmotactic responses of many insects and other animals and such plants as *Mimosa*. The reaction is segmental and not controlled by the supra-oesophageal ganglion.

MIGRATIONS

Osburn (69) has a short note on the migration of dragon-flies and Barber (7), one on the migration of Myrapods.

About five years ago, Zetek* devised a method of marking insects with an aniline spray and a means of diffusing it out from captured individuals. Parker (73) makes use of this method in studying the dispersal of the house-fly in cities: 1,056 flies were captured at from 50 to 3,500 yards from their breeding place, thus demonstrating what wide range of territory may be infested from a single infested locality.

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* Determination of the Flight of Mosquitoes. *Ann. Antom. Soc. of Amer.*, 1912, vol. VI, pp. 5-21.

Although there have been some dissenting voices, the large swarms of monarch butterflies and of certain dragon-flies seen flying southward in the fall and northward in the spring have been considered seasonal migrations; but, in the past, there has been no such intensive study of insect migrations as has been devoted to bird migrations. Partly as a result of observations made on our Atlantic coast, partly due to extensive reading, Shannon (97) concludes that dragon-flies, the monarch butterfly, the great sulphur and perhaps other insects migrate in certain definite routes which coincide with those followed by migrating birds. These routes seem to be a function of the physiographic features of the country. In the U. S. A. he maps four routes: (1) Extending along the Atlantic coast from Canada to the Gulf of Mexico. (2) Extending along the northern shores of Lake Ontario and Lake Erie and then down the Mississippi Valley. (3) Extending along the western shore of Lake Michigan and then down the Mississippi Valley. (4) Extending along the western shore of Lake Superior and then south along the Great Plains.

MISCELLANEOUS ACTIVITIES

Disease Spreading Activities.—Articles on the relation of insects to the spread of diseases have appeared by Brittain (11), Cummins (21), Fitzsimmons (31), Hindle (46), King (57), Payne (76), Roberg (87), Studhalter (102), Townsend (106, 107, 108), and Zetek (120).

Locomotion.—Amans (3) describes the method of flight of the cicadas and King (56) of the locomotion of *Pterodontia flavipes.*

Parasitism.—Parasites have been discussed by Good (37), Graham-Smith (38), Packard (71), Phil and Nellie Rau (83), and Weidman (115).

Phosphorescence.—Notes on the synchronous flashing of fireflies have been published by Allard (2) and Morse (65).

Respiration.—d'Orchymont (68) describes in detail the methods of respiration of certain aquatic insects.

Pollination.—Nägeli, Bonnier, Schroeter, Mrs. Soth and others believe that there is a scarcity of insect visitors to flowers above the timber line. Kenoyer's (55) studies lend themselves to a different interpretation. "Selecting comparable weather and excluding the honey-bee, which does not live at high altitudes, it seems to me that the flowers above the timber line are as much visited by insects as those of lower altitudes, and I have no reason to suppose that they are less dependent for pollination upon their insect visitors." His view harmonizes with those of Muller and L. H. Pammel.

Temperature Effects.—Back and Pemberton (5), Phillips and Demuth (78), and Pierce (80), have discussed the effects of temperature upon insects.

SLEEPING BEHAVIOR

In the past very little attention has been paid to the sleep of insects. The Raus (84), by making a careful field study of the sleep of more than a hundred species have partially remedied this defect in our literature. Lack of space prevents an adequate consideration of the contents of the article. It is thought that the following extract from their summary will prove of interest: " The sleep of an organism signifies more than a mere pause in its activity while darkness covers it; while we have not in the present paper touched on the physiological phenomena of their sleep, we have found many interesting associations of this with other activities of the insects. For instance, it is of marked biological interest that a few species certainly seem to choose protectively colored situations, and others select sites which are in various ways protective; that some which are solitary by day are gregarious by night, that some insects sleep with all the regularity of a theoretical modern infant, while others of a more unsystematic life snatch a wink when they can. . . . Vegetable feeders are more frequently regular sleepers, while carnivorous species are irregular. . . . The sleep of animals in immature stages, the larval, pupal or even egg stage, is something untouched upon."

MEMORY AND RECOGNITION

Sell (94) states that the homing of the 12-spotted cucumber beetle is not influenced by a homing instinct.

Rau (82) discovered a leaf-cutting bee, *Megachile brevis*, carrying bits of leaves to a burrow on the southern end of one of the ties of a railroad track. A passing train disturbed her and she seemed to lose her bearings. She searched tie after tie, but always on the southern end only. This caused Rau to conclude that she used the ties as land-marks.

In his studies of the breeding habits of Orthoptera, Turner (111) states that excitement in the presence of the opposite sex is not alone an indication of sex discrimination. "In this state of excitement males will seize other males, members of other species, or even a stick to which the abdomen of a female has been attached. On the other hand there is an entire lack of anything that would indicate excitement in some forms."

TECHNIQUE

Packard (71) discusses methods of rearing the following parasites of the Hessian fly: *Micromelus subapterus* Riley, *Eupelmus allynii* French, and *Merisus destructor* Say.

Dow (26) describes a method of making plaster casts of insect burrows that will interest all students of our subterranean fauna. Mix equal parts of plaster of Paris and water and, by the aid of a paper funnel, pour immediately into the burrow. Three ounces of the mixture are required for *Cincindela*, one and a half for the pepo spider and seven to nine ounces for *Colletes*. It is best to make the cast one week-end and to excavate it the next. In excavating, dig a pit alongside, one foot from the vertical and deeper than the bottom of the burrow. Then, with a stout knife, begin at the bottom and work the dirt away from the cast. If the bottom is not freed first the tube will break. He finds that the species of the tiger beetle can be differentiated by means of their burrows.

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LITERATURE FOR 1916 ON ANTS AND MYRMECOPHILS

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The literature on ant behavior for the year 1916 shows a rather marked predominance in the number of economic papers. In a way this is encouraging for it indicates that the students of economic entomology are tending to place more emphasis upon the general biology of the forms under investigation. Much of the matter in the following pages will be found to have been taken from papers whose point of view is in the main economic.

ECONOMIC RELATIONSHIPS

According to Marlatt (13) the ants that are house pests in North America are, in practically all cases, of tropical origin. Still further, nearly all the ants that have been introduced into North America from Europe and South America, whether house pests or not, are tropical species. In their tropical climate these ants are usually outdoor species but in the temperate regions can usually exist only in houses, green-houses, etc. Most of these ants are annoying rather than harmful, but some of them and especially the Argentine ant (*Iridomyrmex humilis*) are first class pests. Marlatt classifies our ant pests upon a basis of their origin, as follows: Tropical old world ants, 12 species; ants from the new world tropics, 5 species; native North American ants of temperate regions, 2 species.

Of the imported ants whose behavior makes them first class pests, the Argentine ant has, during the past year, received much attention. Donisthorpe (6) states that this species is becoming a serious pest in England. Barber (1) has made a rather extended study of the habits of this ant and speaks of it as being one of the " worst of pests." In the house, he says, it eats everything. The temperature of ice boxes has no deterrent effect and it invades every room in the house. In one case a young baby was attacked with serious results. This ant (1) is also the bane of nurserymen, since it protects aphids in great numbers. The ants build mud shelters over the aphids and see that the young lice are placed on the tenderest shoots.

The summer nest of the Argentine ant is located anywhere (1) but in the autumn the summer colonies tend to concentrate into larger colonies. They cannot stand the wet, freezing conditions of winter in the open, but seek a warm, dry place in which to hibernate. Thus they may frequently be found spending the winter in manure piles or other heat generating rubbish. When these winter colonies break up in the spring, the ants are particularly annoying, as they spread out, looking for summer homes.

In an artificial formicary (1) a queen Argentine ant lays from 3-30 eggs daily. The eggs are immediately taken by the workers and piled with others. Being slightly sticky they cling together and are handled in clumps.

Further ant pests, which may but await importation from the tropics, are indicated in the papers by Mann (12) and Crawley (5). Crawley in publishing notes on the ants from British Guiana, lists a number of species that would seem to be potential house pests. *Solenopsis corticalis* lives exclusively in habitations and is fond of all food stuffs. This species is a severe pest in entomological laboratories. It possesses a powerful sting. *Tetramorium guineense* is a serious pest in cane fields. It stings readily and painfully, and is sometimes so numerous that it is next to impossible for the cane cutters to work in the fields. *Atta cephalotes* kills all kinds of cultivated plants and *Paraponera clavata* possesses a sting that frequently brings on a fever. To give the ants of Guiana full credit one should mention *Ectatomma quadridens*, which lives in the cultivated areas; this species is beneficial in the cane fields as it carries off the larvae of a moth and a weevil borer. It also destroys the egg clusters of the moth. Mann (12) records an instance of beneficial behavior upon the part of *Eciton praedator* which he saw emerging from a commissary building in countless numbers and carrying an "incredible number of insects, mostly cockroaches." Mann, however, lists a number of other species that must possess serious detrimental potentialities should they once gain foothold in temperate regions. Snyder (17) has continued his investigations into the biology of our North American termites and has added many facts of interest to our knowledge of these insects. He has found that white ants occasionally injure living trees and shrubs, in the southern part of the United States. In Florida, they have at times done considerable damage to the newly planted groves of orange trees by eating away the bark and gradually girdling the tree. Similar damage has been reported for apple, peach, pear, cherry, plum, apricot and lemon. In California, pecan, chestnut and walnut are attacked as well. In other parts of the United States a great variety of shade trees are attacked. Snyder says, that all such damage is more likely to occur in new soil or recently cleared woodland, especially in the latter, if the stumps are still standing.

In the south, termites also occasionally injure the stems and roots of a great variety of healthy field crops, both grain and truck; they attack corn, cotton, sugar cane, rice, grasses, potatoes, and garden vegetables. In the prairie regions of Texas and Arizona there is a tube forming termite that lives in the ground and feeds on the roots of the grass. This species is often found under and in, dry cow dung. It has been known to destroy the vegetation over large areas of grazing land.

DISPERSAL OF ANTS

The first colony of the Argentine ant reported for the United States was found in New Orleans in 1891. At the present time there are myriads of colonies covering 1000 square miles of territory and extending from Houston, Texas, to Wilmington, N. C., and from Nashville, Tenn., to the mouth of the Mississippi River (1). Food scarcity hastens the spread of the species. The normal advance under ordinary conditions is from 300-400 feet a year, but rapid dispersal over large areas may take place at times of heavy floods, as the ants will ride in floating rubbish of all sorts. They do not drown easily and when the rising water floods their nests they frequently cluster together to form a compact ball. The immature stages form the center of the ball with the queens and the workers on the outside. As the ball enlarges by the addition of other workers struggling alone in the water, it slowly revolves and thus the mass is aerated. This aeration is automatic and continuous, for the ants on the under side of the ball are constantly striving to get out of the water by crawling to the top. Such balls may attain a diameter of 6-8 inches and may float about for hours in still water. Upon coming in contact with a solid substance the ball breaks up and the ants crawl out. If coal-oil is poured on the water the ball breaks up and the ants soon die.

Wheeler (25) cites an interesting case of dispersal of a tropical ant (*Pheidole feregrina*, New Sp.), a small colony of which was conveyed in a floating log from the main coast of Brazil to San Sebastian Island, which is about forty miles off shore. Wheeler points out, in this connection, that it is not necessary that an entire colony should be transported to ensure the widening of the distribution of the species; one fertilized queen would be sufficient. Dr. Herman von Ihering, who has been experimenting on this phase of ant dispersal, is quoted by Wheeler as saying, that his experiments with bamboo and other kinds of wood, containing ant colonies, have demonstrated that the ants which he used are decidedly resistant to submersion, provided the nest entrances are closed.

Wheeler (20), while going over the Pergande collection of ants, found a series of workers of the Indian ant *Triglyphothrix striatidens*. These workers were collected in Louisiana, where the ant must have been introduced quite recently. The original home of this ant is Southern Asia and Wheeler's is the first record of its occurrence in the United States. The species, according to Wheeler, is now pretty well spread over the tropics. Its introduction into other parts of this country is but a matter of time, if indeed not already accomplished.

Barber (1) states that the greatest means of dispersal of the Argentine ant in the United States is by steamboats and railroads. They will, he says, ride in lumber, fruit, vegetables, etc. For this reason infestation usually starts around the wholesale grocery and commission merchant houses.

CONTROL OF ANT PESTS

The study of the control of any pest is primarily a study in animal behavior. The study of the control of ant pests consists largely, in the discovery of substances that will either repel or poison them. The literature on this subject should, therefore, furnish one with data concerning ant sense organs, their location, sensitivity, etc. However, this rather purely biological side of the problem has not, as yet, received much attention at the hands of the economic entomologist, who for the most part, finds that he must look for results rather than causes and explanations.

Gibson (9) states that one or two applications of sodium fluoride, dusted in cracks, etc., will cause the species *Camponotus pennsylvanica* and *Cremastogaster lineolata* to leave an infested house. The author believes, but has not demonstrated, that the same remedy will work for other species as well. Horton (10) gives several recipes for anti-ant bands. Sulphur and $HgCl^2$ are the primary ingredients recommended and it is stated that ants can be kept out of trees and cupboards for from 2-5 months with one application. Marlatt (13) says sticky bands do not prevent the Argentine ant ascending trees, for it at once builds a bridge of dirt across the band. The Argentine ant will avoid a quick poison and is repelled to some extent by it. Ant bands containing $HgCl^2$ act as a repellent and are recommended.

RELATION OF ANTS TO OTHER SPECIES AND TO OTHER INSECTS

Myrmecophily.—On April 19, 1915, Donisthorpe (7) captured a specimen of the beetle *Myrmedonia limbata*, which he found running with a number of *Lasius nigra* workers, on the sand bank in which the ant's nest was located. Donisthorpe also records collecting a spider (*Micryphantis beatus*) that looks so nearly like the workers of *Tapinoma erraticum* with which it was running about, that he at first took it to be an ant. This same author has a nest of *L. umbratus* in which an individual of the beetle *Amphotis marginata* has lived for one and one-half years. He records, also, data concerning the behavior of *Myrmica scabrinoides* toward the lepidopterous larva *Lycaena arion*. This larva it appears is not molested by the ants although it eats their eggs and larvae.

Crawley (4) attempts to show that the claviger beetle *C. testaceus* is more strongly attracted toward the queens of *Lasius umbratus* than to those of *L. flavus*, which latter is the normal host. He says, that when he placed a number of the beetles into nests containing *L. umbratus* queens, they clung to the queens and did not seem to change their resting place for weeks. He thinks that it is probable that the parasitic queens (*L. um-*

bratus, *L. fuliginosus* and others) have a body secretion which renders them attractive to the myrmecophils and to other species of ants.

Donisthorpe (7) does not agree with Crawley in believing that the claviger beetles are attracted more strongly by the parasitic queens than by the queen of their normal host; he thinks rather, that they cling without preference to the gaster of the queen of any of the species with which they are associated.

Ants and Other Insects.—The relations of ants to other insects, that are not, strictly speaking, myrmecophils, furnishes a wide field for investigation. The literature for 1916 contains many new data bearing on this aspect of ant behavior. Theobald (18) describes a new genus of aphids taken by Crawley in the nests of various species of *Lasius.* Smith (14) records the following species as attending aphids and other insects in South Carolina. *Iridomyrmex pruinosus* he found attending the "green bugs," *Toxoptera graminum;* this aphis was also attended by the ant *Dorymyrmex pyramicus. Prenolepis imparis* attends the black elder aphis, *Aphis sambucifolia*, and also the cottony cushion scale, *Icerya purchasi. Cremastogaster lineolata* and *Prenolepis impari* attend the scale insect on the pine (Toumeyella pini).

An interesting piece of behavior upon the part of a tiger beetle and an ant is recorded by McAtee (11). This author saw the beetle standing motionless in a road with the ant running all over the surface of its body. The beetle, which proved to be *Cicindela unipunctata*, ran actively when the observer attempted to catch it. The ant was identified as *Formica fusca*, var. *subsericea.* Mann (12) in his discussion of the ants of Brazil says that *Platythyrea meinerti* probably lives in termites nests but does not give any information as to whether or not the ants occupy the same galleries with the termites. Crawley (5) also records an ant (*Dolichoderus debilis*) that makes its formicary in the nest of a termite. Termites were still living in the nest but whether or not they mingled with the ants is not stated. Crawley reports that the common leaf cutting ant (*Atta cephalotes*) of British Guiana is accompanied by a muscid fly that laps up an excretion from the tip of the ant's abdomen.

Social Relations of Ants.—The Argentine ant (1) will not tolerate any other species of ant but drives them out before it. Among its own kind, however, it is extremely social and workers from widely separated colonies mix readily. There are usually several queens in any small nest and they live together amicably. In the winter nests there may be several hundred queens and countless workers and immature stages. *Eciton hamatum*, a common Brazilian ant (12), lives largely upon other ants. It attacks particularly *Dolichoderus lugens*, which latter species secretes from the anal gland a large drop of yellow liquid which Mann takes to be protective. Another case of predaceous relationship among ants is suggested by Donisthorpe (6), who describes a new species of *Epitritus* from Hawaii. He states that this species, which he calls *wheeleri*, probably accompanies other ant species and preys upon their brood stages.

Donisthorpe (7) had a colony of *Leptothorax nylanderi* into which, as food, he introduced some worker pupae of *Myrmica scabrinoides*. Some of the pupae were eaten but others were not harmed and the adults emerged in due time. Most of the Myrmica workers were killed at once, but for some reason one was allowed to go unharmed. This individual lived in the Leptothorax colony for three months, when it died an apparently natural death.

Up to the year 1915, according to Donisthorpe, there was only one instance on record where queen ants have been reared from eggs laid in captivity. For five years Donisthorpe had kept a colony of *Myrmecina gramnicola* but no queens were produced. On July 1, 1915, however, three winged females appeared from pupae, which must have been reared in the captive nest. By July 10, fifty winged females were present and many others appeared later. Only one male was seen. No mating was observed but by the end of August many of the females were removing their wings. On September 16, the male was seen flying about in a very excited way in the nest; the next day it was dead.

The winged females helped to carry about the larvae, to kill and cut up flies, and in general behaved as workers. The last one removed her wings December 15 and all the deälated females continued to behave as workers. As to whether or not they will lay eggs remains to be seen. The only explanation which Donisthorpe suggests for the appearance of the sexual forms is that he had fed the colony an unusually large amount of animal food.

Wheeler has stated in previous papers, that if the wings of a virgin ant queen be removed, she will behave like a fertilized queen. This does not seem to have been the case with Donisthorpe's queens which, as just related, behaved like workers after removing their own wings. Crawley has maintained that deälated virgin queens of the genus *Lasius* do not behave as though fertilized. To test this question for *Lasius*, Donisthorpe (7) on September 3rd, 1915, introduced into a queenless *umbratus* colony a virgin *fuliginosus*, from which he had removed the wings. The queen ran around among the *umbratus* workers tapping them with her antennae and was accepted by them. She was cleaned and given the attention due a queen from her workers. On September 7 the nest was left in the sun and some of the workers began pulling the queen about; when the nest was placed in a cool situation the queen was again accepted and on December 19 had not again been attacked. Whether or not a deälated virgin female will act as a queen, probably depends upon more than mere loss of wings. The receptivity of the colony in which she finds herself is undoubtedly important. Crawley (5) points out that the tropical ant *Tetramormimum guineense* has ergatoid females which are only slightly larger than the workers and run about with them.

ORIENTATION OF ANTS

Brun (3) believes he has shown that the higher ants orient by using large distant land-marks; he thinks the lower ants do this also but to a smaller extent. The higher ants, he finds, can complete the hypothenuse of a triangle, even from a considerable distance. This, he says, is not due to kinaesthesia or to a sense of angles but to the utilization of a visibly distant landmark. These same species show some measure of local memory and Brun believes that the recognition of "known localities" is probably a function of a "topochemical" sense, while the choice of direction depends upon memory.

Orientation after transport, according to Brun, depends on the localization of illumination by the compound eyes and is not exhibited if the illumination is bipolar. Ants cannot associate a complex succession of diverse positions of the median plane of the body, and except within narrow limits, there does not seem to be much kinaesthetic sense of attitudes. There is no static sense. Ants are, however, sensitive to gravity and utilize the hints given by the slope of the route. There is (3) no sense of memory of direction as such, for there is no power of orientation except under the influence of the various stimuli mentioned above.

Wheeler (21) noted that on a certain raid made by the Amazon ant (*Polyergus breivceps*) the raiders which were fully 200 feet from their own nest, returned at once in the right direction, with their plunder, although for forty feet the path taken was entirely different from the one over which they had come.

NOISES MADE BY ANTS

Ectatoma quadridens, a British Guiana ant (5), makes a squeaking sound when it is captured. *Daceton armigerum*, another tropical ant, when captured and placed in alcohol emits from time to time a sharp click. *Azteca schimperi* lives in large carton nests built on the trunks of trees (mango). When disturbed the ants swarm out, making an audible rustling noise. *Paraponera clavata* (15) when disturbed comes rushing out making a stridulating noise. Horton (10) says that when the $HgCl^2$ ant bands are placed around the tree trunks many ants are frequently confined above them in the trees. He has seen these imprisoned ants congregate just above the bands and in some way attract large numbers of free ants which collect on the lower side of the band; there they become so excited that they make desperate attempts to cross the deadly area. The author suggests that stridulations by the confined ants attract and excite the others.

SWARMING OF ANTS

Mating.—Gaige (8) records the following dates for the swarming of ants on White Fish Point, Mich.: *Cremastogaster lineolata*, August 27, by hundreds; *Myrmica scabrinoides*, August 10; *Formica sanguinea*, July 8-9; many more females than males. *Camponotus herculanius*, colonies contain winged males and females all summer and swarming occurs from May 14 to August 14. Smith (14) saw *Prenolepis imparis* swarming, March 19, in South Carolina. Wheeler (21) in watching the Amazon ant go out on its slave raids in late July noted that one day a partial marriage flight took place at the same time. This was in the Sierras in Southern California. The author calls attention to the fact that Emery has shown that the fecundated and deälated female of *Polyergus* founds the colony by entering a *Fusca* nest, killing the queen and taking her place. Wheeler suggests that perhaps the *Polyergus* queen stays behind after the raid. Wheeler has made a very interesting observation on the formation of the *Polyergus* colony in that on July 24 he found an incipient colony of this species which was made up of an ergatoid queen, about a dozen workers and two dozen slaves. The ergatoid female is wingless but apparently can function as a queen. Dissection shows that she has the same organs as the winged queen form. If she is not fertilized, only male progeny will be produced but she may be fertilized, either inside or outside the nest.

Wheeler (19) publishes the first full account of the swarming of the Australian bull-dog ant, *Myrmecia sanguinea*. During the last week of November, he states, there were no winged males or females in the nests of this ant, but plenty of larvae and small numbers of worker pupae. The lack of winged forms was surprising (19) as the sexual forms of most of the ants of New South Wales are to be found in the nests in late October and early November. It was found later, that the sexual forms of the bull-dog ant do not mature till January. They were observed to swarm on January 30 after some very hot, stormy weather. The winged forms were present by thousands and were flying and crawling about in the bushes where copulation was taking place. There were apparently hundreds of males to one female; result, every female was surrounded by a mass of males as big as one's fist. The balls of ants were continually breaking apart and new ones were forming. These ants, which ordinarily are exceedingly pugnacious and can clearly discern objects several feet away, paid no attention to the observer. A similar flight of this ant is described as taking place in early April, in South Australia.

Wheeler (19) points out that these observations prove that the species of the *Ponerine* genus *Myrmecia* celebrate a regular marriage flight like all the ants of the other taxonomic subfamilies, except the species with wingless males and females. The flights occur in January in Northern New South Wales and a few months later, farther south, in the colder parts of Australia. Wheeler has observed that the fertilized females of this species lose their wings and found a colony just as do the higher types of ants.

Snyder (16) says that when termites swarm for the mating flight they do not fly more than 75-100 feet from the original colony. It is of interest to note that with the termites copulation between the royal pair is repeated at irregular intervals over several years. There is apparently no adaptation, as in the ants, for keeping the sperm alive indefinitely in the queen's body.

Swarming for slave raids.—Wheeler (21) camped during the summer of 1915 near Lake Tahoe in the Sierras in California. His camp was situated at an altitude of from 6,000 to 7,000 feet. During the summer he had the opportunity of witnessing several of the slave raids of the western Amazon ant (*Polyergus breviceps*). The slave was always an "ill-defined" variety of *Formica fusca*. Wheeler found that these raids always took place between 3:00 P. M. and 5:30 P. M., on warm days, during the latter part of July. The *Formica fusca* colonies usually tried to resist the Amazons by plugging up the nest entrances with pellets of earth; in one case the *fusca* ants fought so valiantly that the battle raged for 30 minutes and until most of the defenders had been killed. Before starting on the raid, the *breviceps* ants came out of their holes and congregated about the openings. Then at some indistinguishable signal they usually hurried off greatly excited. Winged females were seen to accompany the workers and in some cases they entered the *Fusca* nest but usually did not return with the pupa-laden workers.

On one raid part of the army plundered a small nest and returned home with the plunder, while most of the army went on. In one attack where the *Fusca* ants defended vigorously, part of the Amazon ants fought while others kept digging at the earthen barricade which the *Fusca* ants had thrown up. On this particular raid several deälated females were seen to return with the workers but they carried no plunder.

On July 30 the ants made no raid and the weather was cloudy and much colder than on previous days. A number of winged males were constantly coming to the opening of the nest but most of them were dragged violently back by the *Fusca* slaves. A few escaped and flew away. Wheeler says that the slaves were very active at the entrances to the nest and seemed to be keeping the worker Amazons from making a sortie.

Wheeler points out that the raids here described took place about two hours later than those recorded for the same and other species in Colorado, Illinois, Pennsylvania, and New York. He is inclined to believe that temperature and humidity in some way regulate the time and day of the raid. The optimum temperature for such raids he thinks is near 70 to 75 degrees F. Wheeler states that future descriptions of Amazon expeditions should be accompanied by accurate temperature, barometric and humidity readings. The writer of this review hopes the future investigators will take this suggestion of Wheeler's very much to heart. Furthermore, the procedure which Wheeler suggests should not be limited to slave raids of Amazon ants. Every student of animal behavior should keep an accurate record of the environmental conditions under which the behavior, which he records, took place. This suggestion is particularly applicable to students and observers of insect behavior. Our entomological journals are filled with new and interesting records of observations on insect behavior but in practically no case has the observer taken the time to record for us, the temperature, the humidity, the rate of evaporation or any other of the environmental factors that must have played such a large part in determining the reactions which he records. One need not feel that the recording of such factors makes him an advocate of the mechanistic hypothesis, yet I am afraid that some feeling of this kind does prevent certain entomologists from taking such records seriously. Whether or not organisms are mechanisms does not in the least alter the fact, which would seem to be obvious, but which has also been demonstrated again and again experimentally, namely, that animals in their natural environments are continually reacting to, and in many cases are largely controlled by the stimuli, which impinge upon their receptors from the surrounding environment. Experiment has also shown quite clearly that temperature, light, and rate of evaporation are especially important in the influence which they exert upon the reactions of animals. No observer should consider his field outfit complete until he has added to it a thermometer, an atmometer and a photometer. None of these instruments is complicated or bulky and all can be carried into the field without inconvenience. It is to be hoped that they will come into immediate and general use.

GENERAL FACTS CONCERNING ANT BEHAVIOR

Atta laevigata, a Brazilian ant (5), cuts up leaves and carries them into its nest only at night. It begins work after sundown and quits just before dawn. *Atta cephalotes*, the common leaf-cutting ant, also works only at night, except for a few small forms which may carry sand about during the day. Light seems to play an important part in the lives of these species. Ants in general seem to be very sensitive to light and moisture. Mann (12) records that *Eciton filosum* prefers to travel under ground and when it comes to an impassable barrier constructs an earthen tunnel over it. This behavior is very much like that of the termites which are very negative to light and require constant access to moisture. Snyder (16) says that the center of activity in termite colonies is governed to a considerable extent by the wetness of the season. In moist springs the outlying galleries are teeming with life while in the summer these galleries are too dry to be used. In arid regions termites burrow deep into the ground all the year round, as they do in summer only in moister localities. In temperate regions they enter the ground in October and November and do not emerge till February or March. Termites can work in dry, hard wood and in other dry substances far from the ground, provided there is access somewhere to damp earth. They use a mixture of moist earth and finely digested excreted wood in creating more favorable conditions of moisture and shelter, while extending their galleries. They pass over concrete and brick by means of small shelter sheds which they construct across the obstacle. In the Southwest (Texas and Arizona) there is a species of termite that lives in the grass-lands and is able to live on the grass above the ground by covering the stems with earthen tubes.

Concerning the general habits of termites, Snyder (16) says that in North America they do not construct permanent nests but change their location from time to time. An average colony contains several thousand individuals while an old, long established colony, may be inhabited by tens of thousands. The increase in numbers in a young colony is slow. Snyder further states that termites usually follow the grain when working in solid wood. The tunnels of their nests therefore run parallel to the grain of the wood.

Among other interesting notes on the ants of Brazil, Mann (12) describes the habits of the ant *Pseudomyrma arboris*, which he says lives in trees of the genus *Triplaris*. The natives say that this species never lives anywhere else and never lives on any but the live tree. Also, in all live trees of this genus, the ant is to be found living in the hollow parts of the stem. That the ants protect the trees is easily demonstrated, for they are very pugnacious and possess a painful sting. Whether or not they receive any advantage from the tree, other than that of being furnished a place to nest, is not determined. Crawley (5) describes the ant *Cryptocerus minutis* as being very sluggish and states that it will remain absolutely motionless on a leaf for hours at a time. Smith (15) saw, on April 15, 1916, *Trachymyrmex septentrionalis* out for the first time that spring, in South Carolina. The workers, he says, were taking apple petals into the nest for the purpose of growing fungus on them. Beebe (2) collected and examined four square feet of tropical jungle ground stratum and found 1,000 species of animals therein. Ants made up 30 per cent of this total. Termites were also abundant. Two new genera of ants testify to the unexplored state of this part of the jungle. Most of the ants were found below the surface layer; in fact this middle layer contained four-fifths of all the animals found. The ants were living in small colonies in the semi-decayed twigs. The colonies seem to be complete though there were only 5-15 individuals in any given colony.

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LITERATURE FOR 1916 ON THE BEHAVIOR OF VERTEBRATES

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SOUND

Mammals.—The animal literature this year reflects the popular interest in other psychological fields in that the papers are chiefly devoted to the learning process. There are only two articles to report on sound. One is a timely article by Reuter (22a) which discusses the effect of heavy firing upon animals. He says: " Soon after the beginning of hostilities game began to migrate into Luxemburg, Switzerland, and those parts of France and Belgium which were distant from the warfare. The first to go were the wild boar, badger and bear, followed by the roebuck and red deer. The hare, noted for its timidity, continued in its old territory. The larger birds, grouse, pheasant, sea-eagle and wild duck were driven away, but the song birds continued to build their nests and sing as usual. The house dog seems more resistant to the noise of detonation than do other dogs. But the thoroughbred and halfbred horse is more sensitive than the common horse and the celebrated Russian horses than the German war horses, drawn from all sources, which quickly become inured to the noise of battle."

Peterson (21a) suggests that if Hunter's results prove to be correct, if the white rat is deaf to tones and not to noise, the animal should furnish us with valuable data toward settling the question as to how the ear analyzes the complex vibrations of the air waves. For there must be some anatomical condition which is responsible for the lack of sympathetic resonance in the cochlea of the white rat.

CUTANEOUS SENSITIVITY

Fishes and Amphibians.—The existence of a common chemical sense is still a subject for discussion. Crozier (7) argues for such existence as against Coghill, who thought that the reactions were caused by the use of a high concentration of acids which disrupted the permanently embryonic cells of the germinative layer in the skin of amphibians and fishes. He bases his conclusions upon experimental behavioristic evidence and micro-chemical studies.

Sayle studied (24) the reactions of Necturus to stimuli through the skin. She found it everywhere sensitive to tactile and chemical stimulation, although some parts were more sensitive than others. When any part was fatigued for a given chemical it rarely responded to tactile stimulation although it usually reacted to other chemicals. Both the eyes and skin are photoreceptors and the stimulation of either brings about a negative reaction.

VISION

Birds—and mammals.—Two years ago, it may be remembered, Johnson published the first of an admirable series of articles on visual discrimination in vertebrates. These are followed, this year, by three others (13). The previous experiments determined the width of striae in a field which could be distinguished as striae at a given distance under experimental control. Paper III reports an attempt with the same animals, a monkey and two chicks, to ascertain what differences in the width of two systems of striae, both of which have proved distinguishable, are necessary to effect discrimination. He found that the monkey could distinguish differences in width of striae of less than 3%. This is quite comparable with human ability but roughly is ten times greater than the ability shown by the chick 2. In the next experiment the differences in the direction of the striae furnished the basis for discrimination. The monkey's difference threshold for direction of elements of a pattern lay between 2° and 5°, the chick's between 25° and 40°. The relative improvement brought about by training was much greater in the monkey than in the chick. The third paper gives a carefully controlled demonstration of the dog's deficiency in detail vision and ascribes these factual results to the relative insensitivity of the retina to the differences of distribution of brightness over it.

The spectrum of the domestic fowl is the subject of a study by Lashley (16), who says: "The present paper offers further evidence for the existence of color vision in the fowl, in the form of data upon the relative stimulating effect of different wave lengths upon the light and dark adapted eye, the ability of the fowl to react upon the basis of wave lengths, and the appearance of relatively abrupt changes in the stimulating value of different parts of the spectrum." The Yerkes-Watson color apparatus, with slight modifications. was used and the experiments were subject to a high degree of control.

In a study on the spectral sensitivity of birds Watson (28) says that the limit of the chick's spectrum at the red end lies probably between $\lambda = 7000$ and $\lambda = 7150$; at the violet end, between $\lambda = 3950$ and $\lambda = 4050$. This range is similar to that of man except in the extreme red end. The range of spectral sensitivity in the homing pigeon lies approximately between $\lambda = 4200$ and $\lambda = 7100$.

REFLEX AND RHYTHMIC ACTIVITIES

General.—The conditioned reflex is urged by Watson (26) as a method *par excellence* in psychology. He describes the technique and discusses various phases of the problem, persistence, reinforcement, inhibition, etc., and concludes by sketching ways in which the reflex may be used to obtain differential reactions. Craig (6) would like to know whether we find in animals anything like the synchronism of rhythm exhibited by men as they march or dance or keep step to music. Such a correlation of activities involves a conceptual awareness of the relation of one's own action to that of others. But, the author asks, may not animals have some innate mechanism which would bring them into synchronism with some external rhythm. He examines the evidence for many forms and says that if we reject (1) the slow rhythm due to day and night or seasonal changes and (2) cases in which there is bodily contact with the other rhythmical object as canary and perch or spider and web the case seems good only for the cricket chirping, " And even in that case it is still somewhat in doubt whether their simultaneity is accidental or due to the influence of environment or due to a lock and key adaptation by which one cricket stimulates the other."

Mammals.—The reflex by means of which cats in falling always turn in the air and land on their feet was studied experimentally by Muller and Weed (19). They found that the normal cats which they tested could complete the turn within a one foot fall and some even in six inches. Blindfolded animals did this also but not quite so accurately. They destroyed the semicircular canals in a few animals and these turned also but not quite so perfectly and they required a greater distance. Animals in which there was unilateral destruction turned and landed on their feet, but the turn was characteristic, i.e., always away from the lesion. When these animals with one or both canals destroyed were blindfolded the reflex failed. Only a few with one side destroyed succeeded in turning. Ablation of the motor cortex bi- or unilaterally did not abolish it. It occurred even when blindfolded. Decerebration abolished it. The authors conclude that the reflex depends upon excitation derived from the eyes or the semicircular canals, but their evidence was non-conclusive either for or against Sherrington's theory that the muscles predominantly affected are those which antagonize gravity.

Amphibians.—Howat (12) studied the effect of nicotine on the skin reflexes of frogs. She found that certain spots in the frog's skin differ not only in irritability and reflex action but also in susceptibility to the influence of nicotine. The skin reflexes were affected by much smaller quantities of nicotine than the higher reflexes, e.g., turning over, compensatory and swimming. Small doses of the drug caused a depression of the reflexes and increasing doses brought about a tolerance.

INSTINCTS

Birds.—Watson (27), in the Carnegie Institute publications, has an historical and experimental study of homing. There is an excellent critical account of the various theories of homing, a brief summary of such instinctive activities of the noddy and sooty terns as have a bearing on the question, and a record of the experimental homing flights of these same birds in 1910 and 1913. Some of these flights covered as great a distance as 855 miles. In the same interesting field Cooke (5) has published, in a government bulletin, an account of migration with reference to the weather, the time of day, the distance covered, the routes, the rate of flying, etc. The maps are the most valuable part of this bulletin. They show both the general migration routes on the western continent and the special routes of different species.

Goodale (10) gave some young chicks to different capons who brooded them as hens would have done. There were slight differences in behavior but he says that, although the tests are not extensive, it would appear possible that the brooding instincts of the capon are not necessarily a female character.

Mammals.—The setting reactions of bird dogs to turtles is described by Bingham (2). Montané (18) tells of the instinctive reproductive behavior of an adult chimpanzee from Sierra Leone. The account is extended until after the birth of the young monkey. It is difficult to know whether articles on hibernation should be listed in this place or not. However, Rasmussen (22) has given a brief and valuable summary of the theories of this phenomenon and the paper includes a bibliography of 83 titles.

THE LEARNING PROCESS

Mammals.—Hamilton's laboratory in California probably offers the best facilities available for the study of monkeys in this country. In a Behavior Monograph, Yerkes (30) presents the results of his six months' work at this place. He used his multiple choice method, which has previously been described in this journal, with a *cynomolgos*, a *rhesus* and an *orang-utan*. It will be remembered that of nine entrance boxes, with from three to nine doors open in a prearranged order, the animals, in successive problems, were to choose the first door at the left, the second from the right, alternately the first door at the left and the second from the right, the middle door, etc.

The *cynomolgos* finished two problems, taking over 1000 trials for the second; the *rhesus* finished three and worked over a month on the fourth; and the *orang* finished the first but failed to solve the second in 1300 trials. Some supplementary tests were given and many interesting observations recorded. Professor Yerkes is disposed to insist, unduly it seems to the reviewer upon the basis of his experimental evidence, on ideational behavior—ideational control. He says: "Especially noteworthy, as evidences of ideation, in the results yielded by the multiple choice method are (1) the use by the *orang-utan* of several different methods in connection with each problem; (2) the suddenness of transition from method to method; (3) the final and perfect solution of problem 1 (by *orang-utan*) without diminution of initial errors; (4) the dissociation of the act of turning in a circle from that of standing in front of a particular box."

A briefer description of this work is found in another article by the same author (31) and he gives a fuller account of the multiple choice method in the paper following (32). In *Science* (33) he presses a point which others have also advocated, that provision be made for a permanent field laboratory for the study of monkeys and apes.

Hamilton (11) this year continues his work on the perseverance (trial and error) reactions in primates and rodents. The apparatus had four doors of exit, only one of which in any trial permitted escape. This open door varied with every trial, but in a regular order. There could be no fixed reaction, no definite path to learn, in such a situation and Hamilton's interest lay in an attempt to analyze the varying responses. He found six general types of reactions which we have not space to enumerate, but he says that the different responses were less a species than an individual characteristic. The chief directive agencies are thought to be the spatial relations together with the pull which the recency and frequency of the activities in certain avenues exerted. In regard to recency and frequency the author maintains that, " These studies suggest a possibility which they by no means prove, that with descent of the phyletic scale the factor of recency increases in importance as a determinant of habit formation, whilst that of frequency relatively decreases."

The behavior of a group of monkeys involving the acquisition and control of some very awkward movements and unusual positions in getting food are described by Kempf (14). Another paper by the same author may be mentioned by title (15). And lastly among the many monkey studies appearing during the year is one by Furness (9) who reports upon his efforts to teach monkeys and apes to speak. Two other mammalian studies have been published: one by Meyers (17) on the importance of primacy in the learning of a pig, the other by Burtt (3) giving the results of his use of the multiple choice method with four rats.

Fish.—Maze problems have been used with fish before, but Churchill (4) contributes an account of his work with gold fish in a learning problem with a very simple maze.

QUESTIONS OF INHERITANCE

The behavior of stock and inbred rats was investigated by Mrs. Yerkes (29). She used the circular maze and the Yerkes discrimination box. On the whole the evidence seemed to show a greater facility in learning on the part of the stock (control) rats. The experimenter says: "The inbred rats showed an ability to form the same habits as the stock rats but they did it more slowly and with greater irregularities from day to day."

Another paper on inheritance is that of Bagg (1), called "Individual differences and family resemblances in animal behavior." He used 90 mice and the very simple maze of Cattell. Each individual was given 17 trials, but the first two trials are eliminated from the summaries because, the author says, they are so largely affected by chance. The method of experimentation was loose. The conclusions, which are based entirely on the mean variations in the time records, are, that the resemblances between individuals of the same litter are twice as great as the resemblances between the individuals of the entire group.

The behavior of chicks hatched from alcoholized eggs was the subject of research published by Fletcher, Cowan and Arlitt (8). By alcoholized eggs they mean eggs which had been treated with alcohol before incubating. Among the experiments were those concerned with light, pecking and drinking reactions, and maze learning. From the experiments, alcohol seems to have no specific effects. Such differences as were observed might easily have been due to malnutrition during hatching and could readily be produced by other agents.

GENERAL

Perhaps the most important paper that appeared during the year was Watson's (26) "Place of the conditioned reflex in psychology." The laboratory technique is carefully shown and then there follows a description of the general characteristics of the reflex with methods of dealing with them, ways of using the reflex to obtain differential reactions and finally the range and applicability of the method.

Peterson (21) contributed an additional explanation to the building up of a complex act or, perhaps one would better say, he elaborates a theory which has been implicit in other theories. Briefly, it is this: No partial response in a complex situation can be viewed in isolation, as it grows out of what went before and looks forward in attitudinal impulses to what comes after it. Thus there are mutually reinforcing and inhibiting functions and overlapping of tendencies. And the adoption of the explanation of the complete response would help to explain the checked, impeded, inhibited behavior as well as that which shows reinforcement and also the elimination behavior incident to a successful reaction.

Behaviorism was the title of a paper contributed to the British association for Advancement of Science by Robinson (23). Swift (25) has an article entitled "Some developmental psychology in lower animals and man and its contribution to cer-, tain theories of adult mental tests." And Nesbit (20) has a valuable article, illustrated, describing the photographic outfit and technic for the fascinating undertaking of making wild animals take their own pictures.

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ON THE ABILITY OF ANIMALS TO KEEP TIME WITH AN EXTERNAL RHYTHM

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The habit of keeping time with an external rhythm, as in singing, dancing, and marching, is an interesting and important phase of human behavior. To what extent are similar habits found among the lower animals? A series of notes reporting observations that bear on this question have appeared in *Science*. But some of them have been uncritical, and the whole problem needs to be carefully analyzed.

To begin with, all non-rhythmic activities should be ruled out as having no bearing on the topic. Certain flocks of birds in flight turn this way and that with a speed and a simultaneity which are remarkable to witness. But their turnings do not recur in a regular rhythm; if they did so, they would constitute a very different and much more complex form of behavior.

As to rhythmic activities. All or nearly all animals keep time with slow rhythms, as the rhythm of day and night, and their ability to do so is an interesting topic in itself. But so far as behavior is concerned these slow rhythms belong in a different class from the quick rhythms here discussed, such as those of locomotion, of song, and of the flashing of fireflies. The slow rhythms often have nothing to do with the nervous system; in human consciousness they are not perceived as rhythms; and they may be left out of the present discussion.

As to the rhythms which are under discussion; there are some cases in which it is certain that animals do keep time with an external rhythm, but they are cases in which there is a direct mechanical connection between the moving parts of the animal and the external object with which it keeps time. A familiar example is the swinging of a canary on a swing perch. Some spiders (e.g., Argiope) swing on their webs in a way which seems to show that they time their movements with the rhythm of the web. Newman (8) and Wheeler (10) observed that certain Phalangidae gather in great clusters with their legs interlocked; when some individuals are disturbed they set up a swinging movement which spreads to their neighbors, and gradually the members of the whole colony are brought into synchronous rhythmic movement. Peairs (9) reports that fall web-worm larvae engage in a rhythmic swaying movement which is synchronous in the whole colony; and he argues that it is probable that the rhythm is conveyed from larva to larva by slight movements of the web on which all rest. McDermott (5) mentions the same phenomenon in a web-worm (same species ?). In all these cases one can conceive how the synchronism is attained, without ascribing to the animals anything beyond their well-known powers; for the " imitated " rhythm is conveyed mechanically to the animal's body and to its muscles.

Without such a mechanical transfer, it is a question whether animals below man have ever been really observed to keep time with an external rhythm. A number of naturalists, as quoted below, claim to have observed such synchronous rhythms; but none of their reports are sufficiently detailed and exact to prove that their observations were free from illusion. There are three fertile sources of illusion in this matter, as follows: 1. The observer cannot give his attention equally to a number of objects at the same moment. It is impossible to watch even two moving objects and tell whether their movements are simultaneous, unless the objects are very conspicuous, or very close together, or both. This seems to account for the fact, e.g., that a man writes to me from California asserting that he has seen flocks of geese and of cranes in flight all moving their wings synchronously. Shull[1] makes a similar criticism of a supposed case of synchronism. 2. We all are prone to subjective accentuation, to a subjective rhythm, and to the illusion that this is an objective rhythm. 3. Many of these observers report a " high degree " of synchronism. Now, unless the synchronism is perfect, unless is includes *all* the animals under observation, the observer is liable to a statistical fallacy. For example, where a large number of fireflies are flashing at slightly different rates there must be a great amount of accidental synchronism; to determine whether there is a degree of synchronism not due to the laws of chance, one would need to make a statistical examination, unless the fireflies are all in perfect synchronism.

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[1] Shull, A. F. The Stridulation of the Snowy Tree-cricket (*Oecanthus niveus*) *Canadian Entomologist*, 1907, **39**, 213-225.

Only one detailed and exact study of the problem is mentioned in any of these reports, or is known to the reviewer. It is Shull's[2] study of the chirping of crickets. Shull timed the chirping accurately in a large number of cases. He verified the law that the rate of chirping increases with the temperature, that at a given temperature nearly all the crickets chirp at almost exactly the same rate, so that there is necessarily a great deal of accidental synchronism. He singled out two individual crickets, to observe whether they really influenced each other and thus produced perfect synchronism, and he gives evidence indicating that this does occur, but the conclusion is stated with some reservation.

A number of naturalists write of fireflies flashing synchronously. But, of the contributors to the present discussion, none had observed this phenomenon more than once; Allard (1), Bumpus (quoted in 7 and in 3), and Morse (6) each had observed it once, and not under circumstances favoring critical observation. Blair (2) and McDermott (5) had never seen it themselves. Doctors S. O. Mast, W. M. Wheeler, and F. X. Williams tell me that they have never seen it. Laurent (4) says that many times in his own observations he has proved that what appeared to be synchronous flashing of fireflies was an illusion due to the twitching of his eyelids. And even in the reports that are given, the synchronism is ascribed to a large and indefinite number of fireflies, some reports even state definitely that the synchronism did not include all the individuals; hence none of the observations are known to have been free from the statistical fallacy mentioned above.

Wheeler (10) believes that a flock of pelicans in flight keep time with each other in their wing beats. In a letter which he kindly wrote to me in answer to inquiry, he says in part: "These birds fly in small flocks of four to eight individuals, if my memory serves me. These flocks are very compact, the birds flying in a single line coincident with the direction of flight, and not oblique as with geese. The beat of the wings was evidently set by the first bird, and sometimes there was an imperfect synchronism until the flock got under way. I am sure that the synchronism was not an illusion. I am also sure that it could not be ascribed to chance." Now, when geese fly in a flock, each goose flaps its wings at its own rate, and thus is free to increase or decrease its speed; even so, the military precision with which geese form in line when moving at high speed through a fluid medium is a remarkable accomplishment. If pelicans can maintain a still closer line while at the same time each pelican beats its wings never faster and never slower than the leader, this is a most astonishing feat, more skillful, probably, than any synchronous rhythmic locomotor activity of human beings. If Wheeler is correct, his observations should certainly be verified and the phenomenon studied in detail by means of photographs and cinematograph films showing flocks of pelicans in flight.

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[2] *Op Cit.*

Wheeler (10) suggests that animals exhibit "a kind of 'Einfühlung,'" but this term is surely inappropriate. He mentions also "a fine sense of rhythm." But it has not yet been proved that animals below man can clearly perceive a rhythm. An ex-cavalry officer writes to me that he regularly observed during parade that the moment the band began to play all the horses at once adjusted their step and forthwith kept perfect time with the music. If this observation were correct it would seem to show that each horse was clearly aware of the rhythm of his own step, of the rhythm of the music, and of the relation between the two. But probably the observation was not correct. On the other hand, if it can be proved that two animals come *gradually* into synchronous rhythmic activity and continue in perfect synchronism, as Shull[3] reports, with some reservation, for crickets, and Wheeler for pelicans, this does not prove that the animals perceive rhythm as such. The least assumption would seem to be that each cricket has two tendencies: each must have, *first*, a tendency to chirp in approximately a certain rhythm, the rate of which is not greatly different in different individuals; and this tendency of each animal to its own rhythm must be sufficiently plastic to yield to the *second*, which is an innate reflex tendency to chirp on receiving the auditory stimulus from the chirp of another cricket. But even this much has not yet been proved beyond question.[4]

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[3] Op. cit.

[4] Since this review went to press the following additional note has appeared. Gates, F. C. Synchronism in the Flashing of Fireflies. Science, N. S., 1917, **46**, 314. This writer arrives at the conclusion that "complete synchronism in the flashing of a group of fireflies is simply a very rare accident."

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SMITH'S "MIND IN ANIMALS"[1]

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The preface states that the book was written to present a brief account of the modes of procedure of animal psychology, its aims, trend and the general nature of the results obtained. Animal psychology concerns the systematic or experimental investigation of the brute mind.

The first chapter is entitled Protozoan Behavior. The variability or trial and error characteristic of primitive behavior is emphasized while the evidence in favor of retentiveness in these lower forms is not regarded as conclusive. Physiological or motor retentiveness evident in habit formation is discussed in the succeeding chapter. The author presents a good analysis and summary of the more important work on the maze or labyrinth problem.

The third chapter is entitled Associative Memory and Sensory Discrimination. Associative memory refers to the derivation by an object of a meaning or significance in virtue of its associative nexus with other activities. It is discussed as a criterion of mind, and its utility in studying discrimination and in testing the strength of a habit or instinct is noted. The larger part of the chapter is devoted to a review of the typical experiments on discrimination.

The following chapter on instinct discusses such topics as their initial imperfection, the generalized character of the stimulus, modifiability, periodicity, deferred instincts, etc. Instinct is identified more with the impulse than with the resultant acts. Instinct achieves certain results but the acts or means may vary. A unity of purpose runs throughout the series of acts. Instinct is thus not a mere chain of reflexes nor can it be explained except with difficulty in terms of reflexes and tropisms. The particular instinct of homing is the topic of Chapter V. Homing is based upon an innate impulse to regain home, which must be supplemented by experience to achieve its end. The discussion is concerned primarily with the experimental factor and the factual material has been taken mainly from the work on ants, bees and wasps.

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[1] The Investigation of Mind in Animals. By E. M. Smith. Cambridge, 1915, pp. lx+194.

There is no general instinct for imitation, though some imitative acts may be termed instinctive. There is a good review of the literature on imitation in the higher animals. The author concludes: "That while under certain circumstances monkeys may, and do, imitate, their behavior as a whole can scarcely be characterized as imitative; nor does imitation appear to play any important part in their learning processes."

The final chapter is entitled The Evidence for Intelligence and for Ideas. It presents a critical analysis of the main experiments and arguments in favor of the existence of ideas and images in animals and the author concludes with the following statement: "Reviewing our evidence we may say that, it is by no means disproved that animals are intelligent and have 'ideas,' but, save possibly for the single exception of Hunter's method of 'delayed reactions,' no test as yet applied, completely excludes the possibility that animal learning is anything more than a process of association on the perceptuo-motor level."

The treatment does not pretend to be exhaustive. Technicalities and controversial questions have been omitted. The work is based almost wholly on experimental data; it reflects wide reading, clear analysis of the factual data and an orthodox judgment as to conclusions and interpretations. This book is well adapted to introduce and orient the general reader to the subject, and it may well serve as a text for the more elementary classes.

WOOD'S "THE FUNDUS OCULI OF BIRDS"[1]

R. M. STRONG
Vanderbilt University

This handsome monograph is a useful addition to the literature of sense organs as well as to ornithology. It gives elaborate and extensively illustrated descriptions of the gross and microscopic structure of certain eye structures for a considerable number of birds. It is especially satisfactory to have such full accounts of the peculiar eye structures of birds, and a morphological basis is furnished for much needed experimental work on bird vision.

Besides the sections on methods, material, etc., there are the following chapters: 4. A Review of the Anatomy and Physiology of the Organs and Tissues seen in the Fundus Oculi of Birds; 6. Ophthalmoscopy of Birds; 7. Macroscopic Appearance of the Fundus Oculi of Birds in Prepared Specimens; 8. Photography of the Fundus in Prepared Eyeballs; 9. Effects of Domestication on the Fundus Oculi of Wild Species; 10. The Ophthalmoscopic and Macroscopic Appearance of the Fundus Oculi in Various Orders of Birds; 11. Classification of the Ocular Fundi of Birds; 12. The Ocular Fundus of Birds in its Relation to a Classification of Aves; 13. Relation of Reptilian to Avian Fundi.

The text figures are well executed and the numerous colored plates are beautifully done. The text print is good. Dr. Wood has been generous in financing the work himself. This interest of a clinician in the pure science bearings of his specialty deserves hearty commendation.

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[1] The Fundus Oculi of Birds, Especially as Viewed by the Ophthalmoscope: A Study in Comparative Anatomy and Physiology. By Casey Albert Wood, M.D. Chicago, The Lakeside Press, 1917; 200 pp., 145 text figures and 60 colored plates.

HOLMES'S "ANIMAL BEHAVIOR" [1]

HARVEY CARR
University of Chicago

The initial chapter contains an excellent account of the history of thought concerning animal intelligence from the time of Aristotle to the modern experimental movement. Then follows a sketch of the evolution of parental care. It develops from reproduction and the first stage involves the selection of a proper environment for the egg. An added step is found in the instinct to store food for the young. Active care for the egg is the next step and this interest in the egg is extended to the young. Parental care is a necessary condition for the development of the family, organized society, altruism, etc.

Three chapters are devoted to tropisms. Much illustrative material is given. The author accepts Loeb's reflex theory of orientation for the more primitive organisms, but trial and error is regarded as the predominant mode of adjustment. There is given an excellent sketch of the factors conditioning the reversals of tropisms and of the proposed theories of explanation.

Three chapters are devoted to intelligence and learning. Associative memory is the criterion of intelligence. Intelligence is derived from the instinctive activities and is not found among the Protozoa. Trial and error is the method of intelligent adaptation. The views of Spencer, Bain and Thorndike on the mechanism of selection are extensively criticised; the principle of congruity of responses is adopted. The primary acts mediate stimuli which excite secondary responses that in turn may either reinforce or interfere with the former. Selection and elimination are the resultants respectively of this reinforcement and interference. The author emphasizes the point that intelligent adaptiveness presupposes some degree of prior adaptiveness and this primary ingredient of purposive responsiveness is found in the congenital activities; in other words intelligence is necessarily a derivative of instinct.

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[1] Studies in Animal Behavior. By S. J. Holmes, Badger, Boston, 1916, 266 pp.

Two chapters are devoted to the relation of form and behavior. Reviewing his own experiments in conjunction with those of Child, he concludes that the behavior of an organism plays but a subordinate though important rôle in the determination of its form. Under the title of Behavior of Cells the activity of many migratory and motile cells is cited. It is suggested that these activities are important in the development of form.

The chapter on Death Feigning describes the wide distribution of this instinct. There are two types,—the cataleptic and the paralytic. The former originated from the thigmotactic response, while the fear hypothesis can apply only to the latter.

The author discusses the sensory basis of sex recognition for various species. He emphasizes the factor of behavior in many forms. The sense used varies with the animal, while many senses may be employed in the higher forms. The fact of sex is important in the evolution of mind. Given asexual reproduction, mental evolution would have been different from what it was. For example, voice,—the instrument of language, functioned primarily as a sex call.

The final chapter describes some experiments on a monkey. The technique and the conclusions are similar to those of most studies on this animal.

In the preface we are told that the present volume is largely devoted to subjects with which the writer's own investigations in animal behavior have been more or less closely concerned. This fact explains the choice of topics and the organization of the book. It was probably intended more for supplementary reading than as a text. Naturally the biological aspects of behavior have been emphasized.

STORY OF GRANNY, THE MOUNTAIN SQUIRREL

CHARLES D. WALCOTT
Smithsonian Institution

When collecting fossils around the west slope of the south ridge of Mount Wapta in 1911 rock squirrels began to come to the quarry we were opening. At lunch time we threw them bits of bread and crackers, and later carried up nuts to give them. They became very tame, and when we returned the following year (1912) one of them that we named Granny, because she apparently had two generations of young squirrels that came with her, would run up on our legs and shoulders, and if we did not promptly give her something to eat she would give a sharp chirp to call attention. One rainy day when crouched under a rubber blanket at lunch time, Granny came and seeing a cake of chocolate lying on my knee made a grab for it, running up my arm and over my shoulder so as to jump to the rocks behind. I made a grab for her, catching her by the end of the tail, which resulted in the snapping of her tail about midway. The following year (1913) she was about again as usual, being easily recognized by her stub tail.

We did not visit the quarry from 1913 until the latter part of July, 1917. Just after a blast had been fired, which was the signal to the squirrels that we were about to eat lunch, we saw two or three of them coming down from the cliffs above. When eating luncheon, Granny suddenly appeared at the edge of the quarry. I called her, " Granny," and whistled as we had in the years before. She immediately ran across the floor of the quarry, jumped up on my foot and ran up my leg, finally sitting up and begging for something to eat as she had done in 1913. There were three strange persons in the quarry, and she would not go near them for several days until she had had opportunity of getting acquainted. The striking feature of this incident is that this mountain squirrel should have remembered through a period of four years and at once ran and jumped up on me as she had been accustomed to doing previously.

Four other squirrels came, two of which were evidently full grown and a year or more old, and two young ones. As Granny disciplined them all when they became too familiar, we supposed that they were members of her immediate family.

After a week or more, Granny became very intimate with Mrs. Walcott and would jump into her lap and onto her shoulders, begging for food. She was entirely fearless, and would cling to a nut or a bit of chocolate and swing in the air until she secured the coveted bit.

When the squirrels first came, they were very thin and extremely active. After a month of feeding, Granny became so stout that she had great difficulty in jumping from rock to rock. Chocolate, nuts, bread and cookies seemed to agree with her, and the day we left the quarry a bountiful supply was placed under ledges of rock, so that they could all take it to their nests which were at the base of the cliffs, about 8,000 feet altitude.

ANNOUNCEMENT TO SUBSCRIBERS

The Board of Editors has decided to discontinue publication of the Journal of Animal Behavior until the unfavorable conditions created by the war shall have ceased to exist.

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